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NATURAL REPRODUCTION FROM SEED STORED IN THE FOREST FLOOR

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PURPOSE OF THE STUDY

On many burns and cut-over areas in the Douglas fir and western white-pine region of northwestern Idaho, Washington, and Oregon there are found dense and irregular stands of young growth, the origin of which can not be traced in any way to the seed trees left after cutting or burning. The effort to find the true source of seed of these stands began with a study [1] to determine the efficiency of seed trees in restocking the ground and the distances to which seed is disseminated.

Studies on the Kaniksu National Forest in northern Idaho of cut-over areas, some with single seed trees and others with groups of seed trees, brought out the fact that western white pine (*Pinus monticola* Dougl.), Douglas fir (*Pseudotsuga taxifolia* [Lam.] Butler), western red cedar (*Juniperus occidentalis* Hook), and western hemlock (*Tsuga heterophylla* [Rof.] Sargent) were producing satisfactory stands of young growth for a distance of not more than from 2 to 5 chains from the seed trees. Instead of being blown abundantly over large areas, the seed was cast in sufficient stand-producing quantities within a radius of only a few chains. This is illustrated in figure 1, which is based on an area studied two years after cutting.

The cut-over area shown in figure 1 contains 160 acres. It was clear-cut, blocks of seed trees (A, B, C, and D) containing from 2 to 4 acres each being left to reseed the area. The slash was left broadcast and burned the same year of the cutting. A very severe slash fire burned over all of the cutting except area E in the northwestern part and area F in the southwestern part. The whole cutting was studied by running

[1] The writer began the study of seed viability and factors influencing germination at the College of Forestry, University of Minnesota. The results of these studies are to be published as a bulletin of the University of Minnesota. He wishes gratefully to acknowledge the assistance given by Mr. D. R. Brewster, of the Forest Service, in this work; also the valuable aid of Mr. C. J. Kraebel, Forest Assistant, Wind River Experiment Station, in analyzing and interpreting the field data.

transects 2½ chains apart. The striking point brought out by the study was the very limited distance to which seed was being carried by the

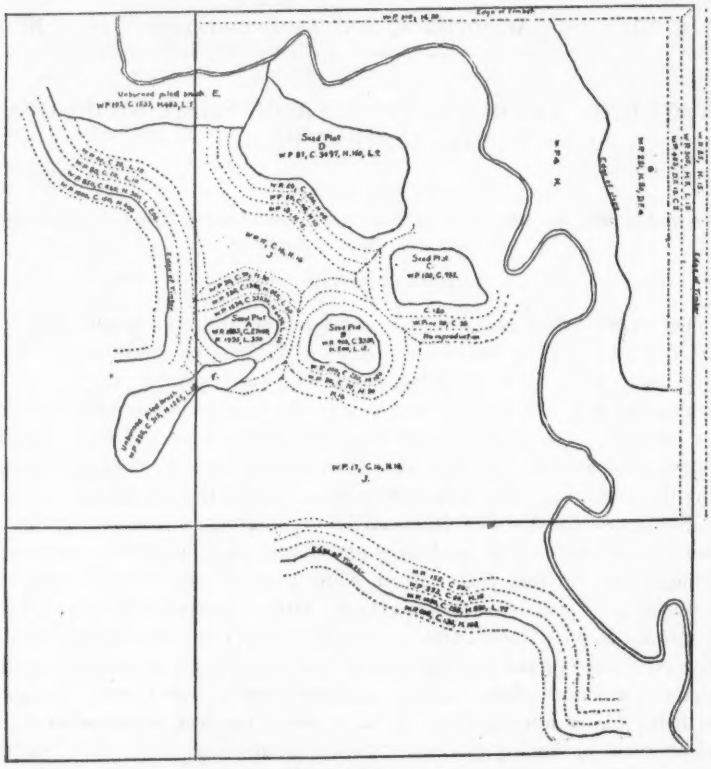


FIG. 1.—Migration chart: Graphic representation of the number of seedlings per acre in each chain distance from seed trees. T. 57 N., R. 5 W., Boise M., sec. 26. Kaniksu National Forest. Scale, 16 inches=1 mile. W. P.=white pine; C.=cedar; H.=hemlock; L.=larch; D. F.=Douglas fir.

wind. The distance of seeding and the effect of the slash fire are shown in Table I.

TABLE I.—*Average number of seedlings per acre at various distances from seed trees on burned and unburned slash*

Species.	Burned slash.				Unburned slash.
	First chain.	Second chain.	Third chain.	All areas beyond 3 chains.	Distances of 3 or more chains.
Western white pine	615	187	40	17	274
Western red cedar	5,600	266	24	16	924
Western hemlock	1,438	195	20	16	854

It is apparent from this table that the seed trees are effective for a distance of only 2 chains on this area, and that reproduction occurs in unburned slash without relation to the distance from seed trees. The limited migration from seed trees threw doubt upon the accepted theory that wind-blown seed is responsible for the dense stands of reproduction occurring in burns at distances of a mile or more from seed-bearing trees. If the seed did not come from the seed trees, then it must have been produced before the burn or the cutting took place, and must have been stored in the duff of the forest floor or in cones. Attention therefore was directed to the leaf litter, and an effort was made to ascertain whether the forest floor of a virgin forest contains any germinable seed of western white pine and Douglas fir. It was found that the duff contains a large number of germinable seed, which might remain dormant there for a number of years and which evidently germinates and results in a dense stand of young growth as soon as the forest is cut down or burned over and light and heat are admitted to the ground.

These facts led to a comprehensive study of large burns, particularly in the Douglas-fir region of Washington, and of cut-over lands in the Puget Sound region. The burns studied were divided into two classes: Areas burned only once were classed as "single burns" and areas burned twice or more were classed as "repeated burns."

The results of the 5-year study from 1912 to 1916 are based on surveys of burns comprising about 750,000 acres, of which 68 acres have been actually examined by the transect method, and about 7,780 acres of cut-over land, of which 22.25 acres have been examined by the transect-and-plot method.

RESTOCKING OF BURNS BY SEED STORED IN THE FOREST FLOOR

THE COLUMBIA BURN, A SINGLE BURN ON WHICH THE DUFF WAS ONLY PARTLY DESTROYED BY THE FIRE

The Columbia burn (locally known as the Yacolt burn), extends northward from the Columbia River on the Columbia National Forest in southern Washington. The Columbia fire burned over an area of 604,000 acres in the foothills on the west side of the Cascade Mountains at elevations varying from 500 to 4,000 feet (Pl. 1). At the lower altitudes the forest traversed by the fire was the well-known Douglas-fir type, which includes the associates, western hemlock, western red cedar, western white pine, and lowland or "grand" fir (*Abies grandis* Lindl.). Above 1,100 feet, silver fir (*Abies amabilis* Forbes) makes its appearance, and then noble fir (*Abies nobilis* Lindl.), until at about 3,000 or 3,500 feet the forest developes the true fir type, composed almost entirely of noble and silver fir with a slight admixture of western white pine and Douglas fir. Pacific yew (*Taxus brevifolia* Nutt.) is distributed almost throughout the forest, avoiding only the subalpine summits of

the higher ridges. Dwarf juniper (*Juniperus communis* L.), on the other hand, is restricted to the subalpine summits.

The fire occurred from September 8 to 12, 1902, following an exceptionally dry season, and, driven by a dry southeast wind, traveled from southeast to northwest. So far as can be determined from local information, it traveled at perhaps a maximum rate of 8 miles an hour during the time it was doing the most damage. No portion of the area has been burned over by a second fire.

The main feature that is now of interest on the burn is the good stand of young growth almost uniformly covering the area and of the same species as that which made up the burned forest. The presence of this reproduction is very obvious to anyone passing through the area, but the reason for its appearance after so severe a fire is a question that has always been open to conjecture. The problem, then, was to determine the history of the reproduction and, so far as possible, to account for its distribution.

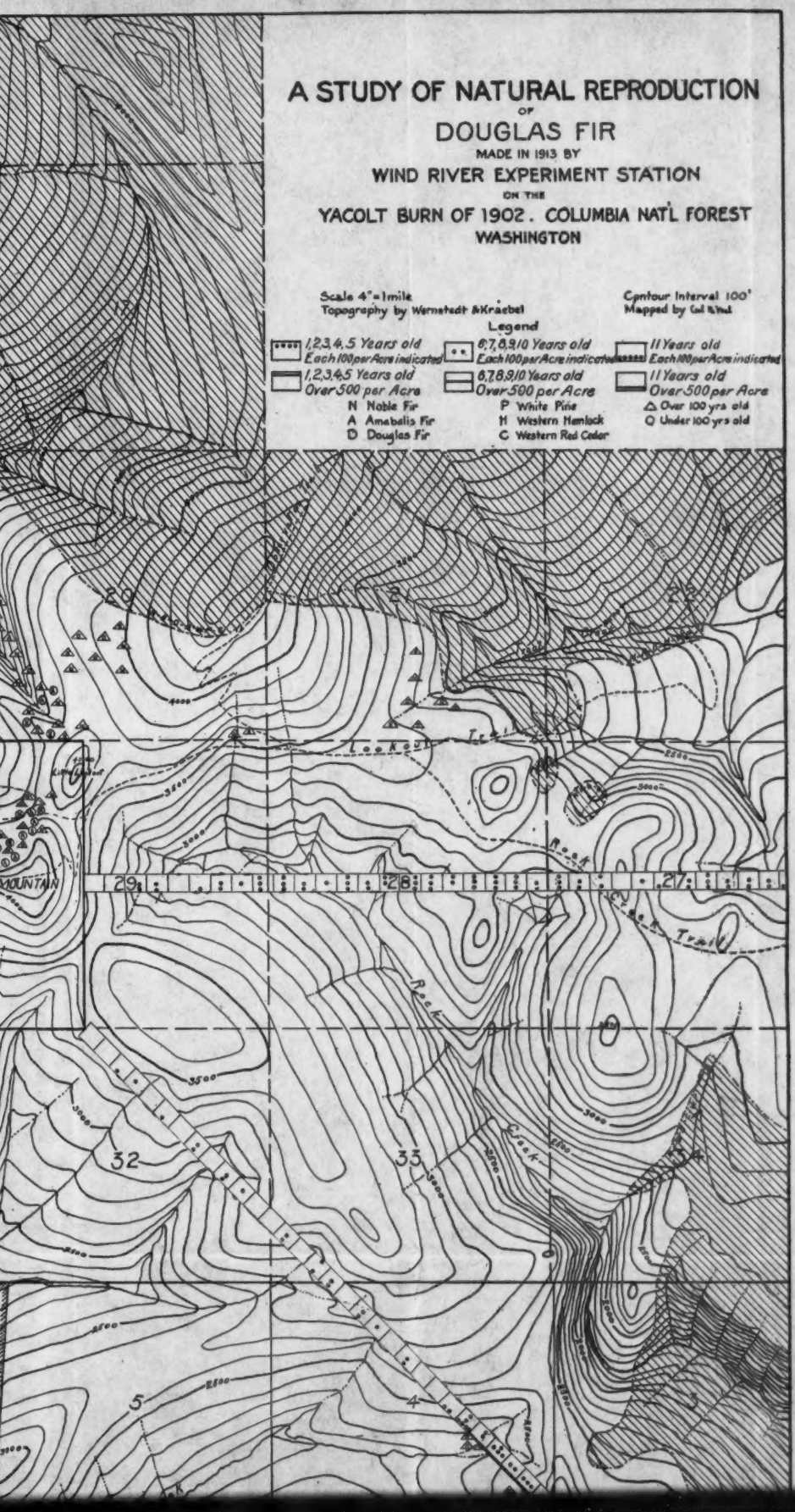
An arbitrary section, chosen to include Lookout Mountain, was studied intensively by a gridiron system of east and west belt transects (Pl. 2, B). These were run 2½ chains apart over the entire section. Then, with this section as a hub, an arbitrary township surrounding it was studied extensively. For this study eight transects were run radially from the centers of the four sides and from the four corners of the section to the corresponding points in the township. Wherever a solid body of green timber was encountered, the transect was discontinued at that point. These belt transects served effectively to disclose the distribution of reproduction over the entire township. The plan of the survey is shown in figure 2. The lines radiating from the center section represent the transects which were run in making the township study.

Each species found on the Columbia burn is discussed separately.

SEED TREES LEFT ON THE BURN ONLY A MINOR FACTOR IN REPRODUCTION AFTER THE FIRE

DOUGLAS FIR.—The Douglas-fir records bring out the fact that there is scarcely any young growth on the south and east slopes of Lookout Mountain, and such as does occur is confined to the draws below the barren slopes. On the north and west slopes, however, it is uniformly scattered. This distribution of the young growth is due to the local topography. The fire approached the mountain from the southeast and naturally swept up these slopes with unusual intensity; also the south and east slopes were hot, dry sites after the fire, and were consequently unfavorable to the establishment of seedlings. On the other hand, on the north and west slopes the opposite of these conditions obtained—that is, the fire was less intense, and the site was inherently more propitious for seedling growth.

14
18
Lewis River
23
24
18
Poison Gulch
Texas
26
25
30
LOOKOUT MOUNTAIN
Trail
35
36
31
2
6


A STUDY OF NATURAL REPRODUCTION
OF
DOUGLAS FIR
MADE IN 1913 BY
WIND RIVER EXPERIMENT STATION
ON THE
YACOLT BURN OF 1902. COLUMBIA NAT'L FOREST
WASHINGTON
Scale 4"=1mile
Topography by Wernstedt & Kraebel
Contour Interval 100'
Mapped by Col & Vail
Legend
1,2,3,4,5 Years old Each 100 per Acre indicated
6,7,8,9,10 Years old Each 100 per Acre indicated
11 Years old Each 100 per Acre indicated
1,2,3,4,5 Years old Over 500 per Acre
6,7,8,9,10 Years old Over 500 per Acre
11 Years old Over 500 per Acre
N Noble Fir
A Amabalis Fir
D Douglas Fir
P White Pine
H Western Hemlock
C Western Red Cedar
△ Over 100 yrs old
○ Under 100 yrs old
T.4 N.
29
28
27
32
33
5
4
Creek
Trail

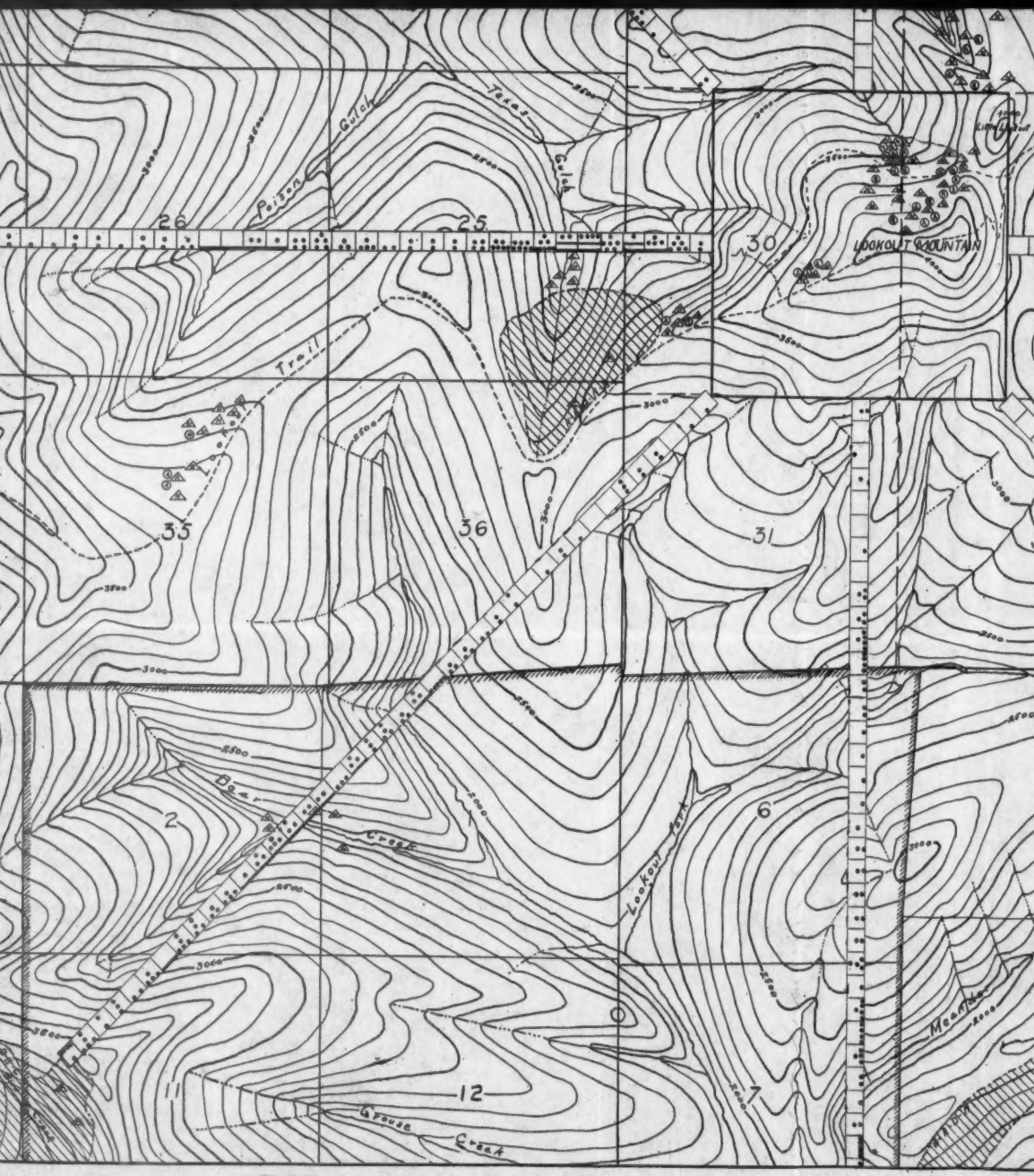
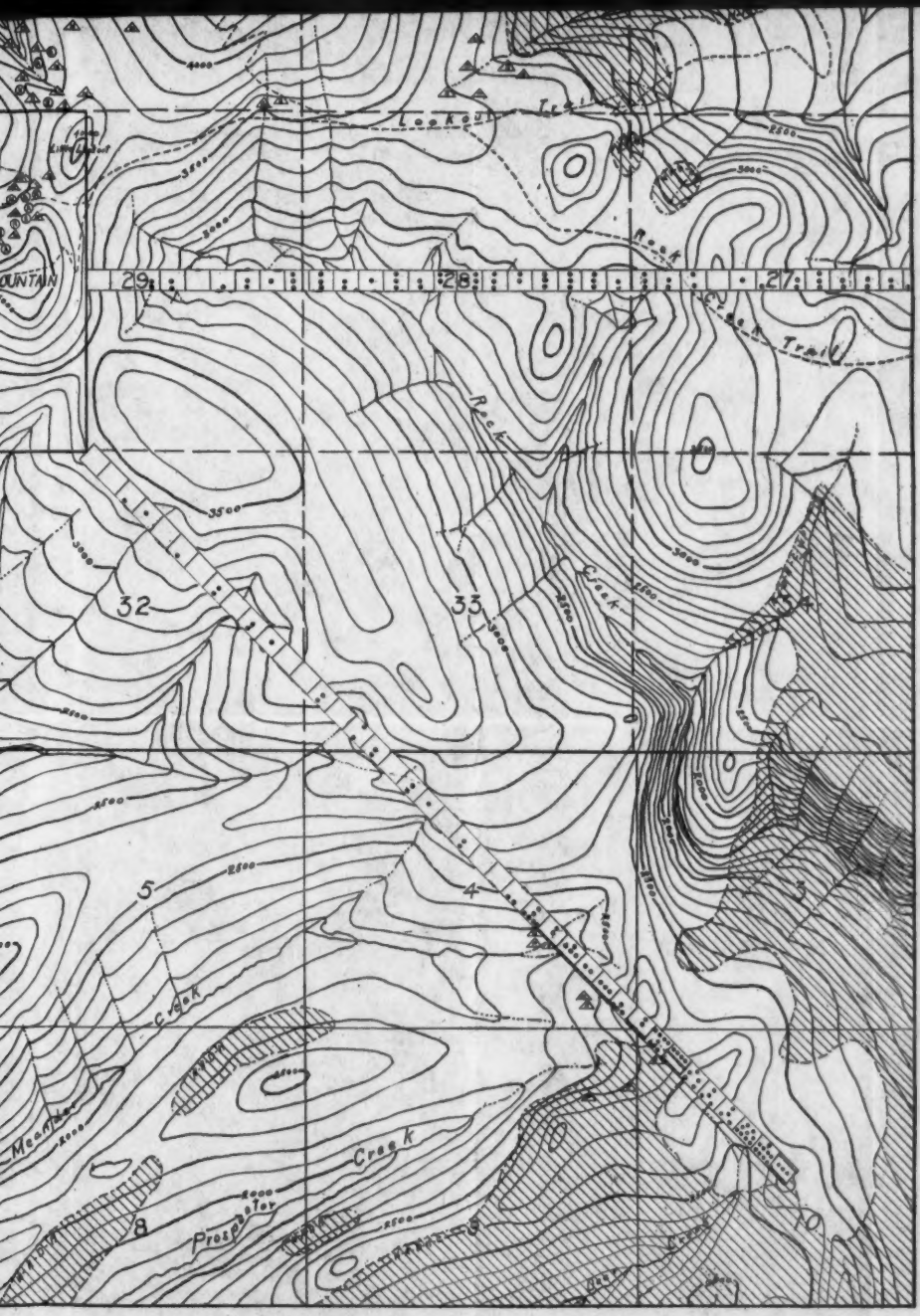


FIG. 2.—Plan of survey on Columbia burn. The lines radiating from the central section indicate the transects run in the study of the township. The cross-hatche

7765°—17. (To face page 4.)



. The cross-hatched areas indicate areas of green timber, and the Douglas-fir reproduction is shown in accordance with the legend.

The most significant facts brought out by the study of the young growth on this section have to do with the distribution of the age classes and their relative proportions, as shown in Table II. This table shows that the 11-year-old class includes 25 per cent of all Douglas-fir seedlings found; the 6- to 10-year-old class, 65 per cent; and the 0- to 5-year-old class, 10 per cent.

TABLE II.—*Classification of young growth on section of Columbia burn studied*[a]

Species.	Distance from seed trees.	Percentage of total area examined included in each distance.	Percentage of total number of seedlings found within each distance.			Grand total percentage of all seedlings found.		
			Over 10 years.	6–10 years.	0–5 years.	Over 10 years.	6–10 years.	0–5 years.
	Chains.							
Douglas fir	Over 10	79.0	61.1	38.2	0.7	25.3	64.6	10.1
	6–10	9.7	48.1	33.3	18.6			
	0–5	11.3	67.6	14.6	17.8			
Western white pine	Over 10	100.0	15.8	84.2	.....	15.8	84.2	.....
	6–10	.....	.....	.....	.....			
	0–5	.....	.....	.....	.....			
Noble fir	Over 10	64.2	96.0	3.3	.7	93.9	3.5	2.6
	6–10	20.4	90.0	5.4	4.6			
	0–5	15.4	76.5	9.4	14.1			
Silver fir	Over 10	56.6	87.9	10.2	1.9	80.1	13.2	6.7
	6–10	24.4	71.5	18.7	9.8			
	0–5	19.0	55.1	22.9	22.0			
Western hemlock	Over 10	92.0	36.8	57.8	5.4	21.8	65.6	12.6
	6–10	8.0	.....	76.9	23.1			
	0–5	.....	.....	.....	.....			

[a] Total area examined=18.6 acres.

The proportion of age classes tells the history of the reproduction, showing that only a comparatively small percentage of the total Douglas-fir reproduction on this area started the first year after the fire, by far the greater part of the seed germinated during a period of from 2 to 6 years, and very little germination occurred in the period from 7 to 11 years. The decrease of germination of seed throughout the section after the first few years subsequent to the burn and the very small percentage of the young age classes found at more than five chains from seed trees indicated that the remaining seed trees had not been a factor in the restocking of the area.

These facts are supported by the records of the township study (Table III). Although the Douglas fir which germinated the first year after the fire was more than half the total Douglas-fir germination, the small percentage of germination after the sixth year following the fire was evidence that the remaining seed trees were not casting seed over the burn, because germination conditions were still favorable when examined 11 years after the fire.

TABLE III.—*Classification of young growth on township of Columbia burn studied*[a]

Species.	Distance from seed trees.	Percentage of total area examined included in each distance.	Percentage of total number of seedlings found within each distance.			Grand total percentage of all seedlings found.		
			Over 10 years.	6–10 years.	0–5 years.	Over 10 years.	6–10 years.	0–5 years.
	Chains.							
Douglas fir	Over 10	89.9	80.6	7.0	12.4	55.0	33.2	11.8
	6–10	4.6	68.5	14.4	17.1			
	0–5	5.5	54.9	13.4	31.7			
Western white pine	Over 10	98.0	25.3	74.7	.....	24.0	76.0	.....
	6–10	1.0	20.0	80.0	.....			
	0–5	1.0	20.0	80.0	.....			
Noble fir	Over 10	89.7	94.1	3.0	2.9	91.4	3.7	4.9
	6–10	5.5	90.9	2.2	6.9			
	0–5	4.8	67.2	8.8	24.0			
Silver fir	Over 10	85.2	93.5	5.1	1.4	92.0	6.8	1.2
	6–10	5.5	75.0	25.0	.....			
	0–5	9.3	80.0	20.0	.....			
Western hemlock	Over 10	78.4	26.5	53.0	20.5	24.4	51.7	23.9
	6–10	9.3	25.0	45.8	29.2			
	0–5	12.3	19.3	51.6	29.1			

[a] Total area examined = 32.25 acres.

The section and township records demonstrate that the occurrence of the age class 0 to 5 years is limited to the vicinity of seed trees or to localities which are topographically within the influence of these trees. Trees on a hillside above a canyon disseminated their seed over a wider range of territory than trees on level land, since the seed could be blown both down into the canyon over the nearer slope and also across to the opposite slope.

There are no Douglas-fir seed trees on the section, except a single broken-topped one, but there are Douglas-fir seed trees within two or three chains of the northeast boundary of the section on the northwest slope of Little Lookout Mountain. These are from 100 to 300 feet above the areas containing the 0- to 5-year-old class of reproduction; hence, it is entirely possible that they are responsible for the occurrence of this age class in the northern part of the section. The limited distribution of the 0- to 5-year-old class, with reference to seed trees and topography, is consistent throughout the section and is particularly conspicuous at several points in the township (fig. 2).

The transect from the west-central point of the section passes within two chains of green timber. The influence of this timber is shown in figure 2 by the occurrence of the 0- to 5-year-old class for a distance of a few chains in the immediate vicinity of the seed trees in Texas Gulch. The remainder of the transect has a scattered stand of reproduction of the older classes, a very dense stand occurring in Poison Gulch almost 1 mile from the nearest seed trees. This same condition is illustrated

on the southwest transect, where the young growth of the older classes is very heavy along the north slope of Bear Creek Canyon at a distance of more than a mile from the nearest Douglas fir timber. The occurrence in this locality of a small group of living trees (noble fir) demonstrates the abatement of the fire as a feature coincident with the subsequent occurrence of dense reproduction. The importance of the relation between the severity of the fire and the amount of subsequent reproduction is developed later. As the transect approaches the timber at the top of the ridge, older seedlings are again very scattered, and it is only very close to the edge of the timber that the younger seedlings begin to appear at all. This peculiar distribution of the reproduction can be observed on all of the transects, and shows very definitely that the green timber remaining after the fire has had very little influence on the general occurrence of the Douglas fir reproduction over the burn.

NOBLE FIR.—The noble-fir records for the section bring out the same points as the Douglas fir records, but in a more striking way because the site was more suited to noble fir than to Douglas fir. It is noticeable that the reproduction of this species is distributed in good stands with remarkable uniformity over most of the section, in spite of the fact that there are two well-defined groups of seed trees within the section. One departure from this uniformity is the scarcity of seedlings on the high south and east slopes of Lookout Mountain, which is undoubtedly due to the dryness of the site and the direction of the fire. On the west and south slope of the mountain extremely dense stands occur, amounting in several places to 20,000 or 30,000 seedlings per acre.

There is another departure from the uniformity of the noble-fir reproduction which is inconspicuous but very significant. This is the restricted distribution of the age class 0 to 5 years, which is limited either to the proximity of the groups of seed trees or to favorable situations downhill from these trees. Even in such places the young class forms only a small percentage of the total reproduction, and decreases rapidly with the increase in distance from the seed trees. These facts can not be construed otherwise than to indicate that the seed-tree groups are not casting their seed for any great distance, in most cases only from 2 to 5 chains.

On the other hand, the older classes, especially the 11-year class, occur at distances of from 10 to 50 chains from the groups of seed trees. Over the whole section almost 94 per cent of all noble-fir reproduction started the first year following the fire, less than 4 per cent in the next five years following the fire, and only 2.5 per cent later than six years, most of this latter being within 5 chains of seed trees (Table II).

The township study shows that noble fir occurs on all of the areas on which it grew before the fire. Some parts of the burn are below the noble-fir zone, and for that reason do not show any noble-fir reproduction. Wherever the species does occur in the township, it was

found that the proportion of age classes is practically the same as in the central section, over 90 per cent being in the 11-year-old class. The distribution of the age classes with reference to seed trees was found to exhibit the same peculiarities as were found in the section—namely, the seedlings under 5 years old are found only in the vicinity of seed trees, seedlings from 6 to 10 years old are more widely distributed over the burn, seedlings 11 years old are found everywhere in the burn where noble fir formerly grew, often forming dense stands at great distances from seed trees that survived (Table III).

These facts show clearly that all the young growth could not have come up from the seed scattered by the seed trees which have survived the fire. The restricted distribution of the youngest seedlings, which so definitely points to their having originated from the seed trees, makes it impossible to attribute all of the older classes to the same source. Had both classes come from the same seed source they would of necessity have exhibited the same distribution.

SILVER FIR.—The silver-fir records resemble in every respect those of the noble fir. In the same groups with the noble fir there are some silver-fir seed trees, the influence of which is about the same as described for the noble fir. The silver fir is found on all sites in the township where it occurred in the forest before the fire, although the silver-fir zone is still more limited than that of the noble fir to higher elevations and cooler slopes.

WESTERN HEMLOCK.—The area studied as a whole is above the western hemlock zone, but young growth occurs in several localities, although usually in sparse stands. The important point about the hemlock reproduction is that burned hemlock trees were found in every locality where stands of hemlock reproduction occurred, and the relative proportion of hemlock reproduction to other species is approximately the same as the proportion of hemlock in the original forest. For example, the transect running from the northwest corner of the section goes through a dense stand of hemlock reproduction at about half a mile from the nearest green timber. This is a favorable hemlock site, and the burned forest consisted of approximately 10 per cent of hemlock. This same circumstance is again evident on the southeast transect at approximately half a mile from the nearest seed trees. On this transect it is also important to note that the heavy stand of reproduction does not continue to the green timber; on the contrary, there is practically no reproduction for 20 chains from the green timber. These facts argue strongly against the theory that the seed source of such isolated reproduction is the green timber which escaped the fire.

WESTERN WHITE PINE.—Western white pine does not naturally form pure stands in the Cascade Mountains of Washington; but individual trees or very small groups of this species do regularly occur in the forests throughout the region. The section and township data for white pine

show a fairly uniform but scant distribution of reproduction of this species over the entire burn, repeating with remarkable fidelity the distribution of the species in the forest before the fire.

A striking fact is brought out by a study of the proportions of the age classes. There was a total absence in the burn of seedlings under 5 years old (Tables II and III). The older classes, however, although sparse in numbers, were uniformly distributed over the township without any relation to the location of possible seed trees. These facts show clearly enough that germination and establishment of white pine in the open burn ceased altogether after the year 1908. This cessation of the appearance of white-pine reproduction was not abrupt but gradual, and is shown graphically in figure 3 by a simple curve based upon the averages of the age-class percentages for white pine in both section and township.

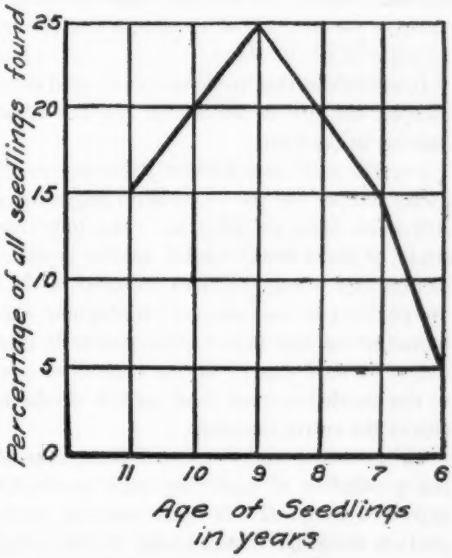


FIG. 3.—Curve showing the germination of white-pine seed in the Columbia burn 11 years after the fire. Note that 15 per cent of the seeds germinated the first year after the fire as shown by the 11-year-old class; the maximum germination of 25 per cent of the seed occurred the third year after the fire, shown by the 9-year-old class, and germination ceased entirely six years after the fire.

The stop in the appearance of white-pine seedlings occurred in spite of the fact that the possible white-pine seed trees in the township continued to produce seed during the four years from 1909 to 1912, and were carrying a crop of cones at the time they were examined in August, 1913. Moreover, the conditions for germination and establishment on white-pine sites over the entire area were still favorable in 1913, and had no doubt been equally favorable during the previous four years. If, then, the existing white-pine reproduction in the burn is attributed to seed transported from surrounding seed trees, why, in the light of the foregoing facts, was there no continued migration and establishment during 1909 to 1913?

In this connection it should be remembered that there were very few living white-pine trees within the township, and that these potential seed trees were always situated within stands of mature timber so that the chance for seed distribution by wind was extremely small. More-

over, with this species, as with all others, the reproduction is uniformly scattered over the township without any relation to the nearness or distance of the possible seed trees. Especially noticeable in this connection are the west, southwest, and south township transects, where white-pine reproduction over 5 years old occurs at a distance of 120 chains from the nearest seed trees. The exceptional quantity of white-pine reproduction near the end of the southeast township transect occurs on a very favorable white-pine site, where the presence of white-pine snags proved that this species had formed an unusual percentage of the original forests. In this particular instance the mature forest contained about 5 per cent of white pine, while the reproduction now constitutes 10 per cent of the stand.

It is obvious that some source of seed other than the seed trees which escaped the fire is responsible for the occurrence of white-pine reproduction in the burn.

PACIFIC YEW AND DWARF JUNIPER.—In the case of Pacific yew and dwarf juniper the theory of wind migration of seed to great distances is still more open to question. The important fact emphasized by the study of these heavy-seeded species is that reproduction is found only in localities where the trees occurred in the original forest. Before the fire Pacific yew was scattered throughout the area, and after the fire the reproduction was found always directly under or beside fire-killed yew snags. Dwarf juniper on the summit of Lookout Mountain grows close to the gnarled mats of dead juniper shrubs and could be found nowhere else in the entire township.

This peculiar and consistent limitation of occurrence argues against the possibility of regarding such reproduction as the result of seed deposited by birds. If birds were the agents of migration, the reproduction would have been found elsewhere than in the immediate vicinity of yew snags or dead juniper shrubs. Careful examination of the fire-killed specimens of both yew and juniper determined beyond doubt that they did not live through and produce seed after the fire; moreover, there are no green trees of seeding age of either species left within the burned areas. Neither of these sources of seed, therefore, can be held responsible for the reproduction of yew and juniper in the Columbia burn.

THE DUFF, THE PRINCIPAL FACTOR IN REPRODUCTION AFTER THE FIRE

The foregoing facts first cast a doubt upon the long-accepted theory of the restocking of large forest burns by the process of wind migration and finally proved it untenable. As the study progressed and this fact grew steadily more convincing, there arose naturally the question, "What was the source of seed for all this reproduction?" The answer to this question also developed naturally through the accumulation of evidence throughout the burn. It was found that the reproduction

most often occurred, not in a solid unbroken cover, but in various-sized patches with very irregular and ramifying boundaries. Where the reproduction was lacking, the ground was covered with grasses, herbaceous plants, and shrubs, evidencing an uninterrupted growth since the burn was formed. The occurrence of these two types of cover made an interlaced pattern resembling mosaic over the entire burn, although each type often expanded solidly over a slope or basin many acres in extent. Everywhere the feature that was most striking was the sharp line of demarcation between the reproduction and the grass areas. For all its tortuous windings the boundary was always distinct. Obviously such a condition could not have resulted from any process of overhead seeding, but must rather have been produced by some action on the surface of the ground itself. The idea of ground fire suggested itself. One who has seen ground fire burning in forest duff will remember that it burns very irregularly, here leaving an island and there forming a deep bay between two points of unburned ground. When at length the smoldering fire is stopped, the result is just such a mosaic of burned and unburned territory as has been described for the reproduction and grass territory. A representative spot in the Columbia burn is shown on Plate 2, A, and the sketch in figure 4 is a graphic portrayal of the same spot.

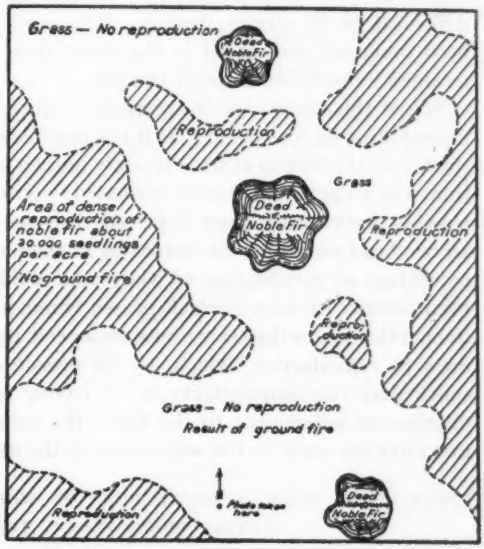


FIG. 4.—Ground plan of the spot shown in Plate 2, A. The conformance of this irregular boundary line with the erratic margin of ordinary ground fire is clearly evident. Constant repetition of this feature over the entire Columbia burn could lead to but one conclusion, that where ground fire burned there resulted no reproduction, excepting in proximity to living seed trees.

The likelihood that any part of the forest floor will burn depends on a number of varying factors, such as the quantity and kind of humus soil and its moisture content. Favorable conditions for a ground fire are shown in Plate 2, C, and the results of ground fire in Plate 2, D. Most severe ground fires occur on dry sites, provided those sites have a sufficient quantity of duff to carry fire at all. Accordingly the reproduction occurs most densely in the moist sites and is open or lacking on exposed dry sites, although this may be partly due to the fact that these

dry sites are very unfavorable to the establishment of seedlings even though germination may take place. Furthermore, irregularity in the areas of young growth occurred on all sorts of sites. This could lead to but one conclusion: wherever ground fire occurred no reproduction appeared, except close to seed trees where seed could be cast upon the burned ground after the fire.

From this it was but a step to the complete explanation: wherever the duff and litter were burned out of the forest floor, there developed an area barren of reproduction; wherever the duff and litter were not burned out of the forest floor, there developed an area of more or less dense reproduction. Therefore, the duff must be the controlling element: the duff must be the storage medium of the seed, and that seed must have been produced and stored in the forest floor before the fire and have retained its viability through the fire.

Before this conclusion is accepted, however, another possible source of seed must be considered. Is it not possible that cones carried through the fire on the crowns of trees severely burned or killed furnished the seed from which the young growth originated? After the fire these cones may possibly have opened and dispersed their seed, becoming in that way an overhead source for the restocking of the burn. In fact, a very small percentage of germination of white-pine, noble-fir, and cedar seed has been secured from seed which passed through a crown fire. But even though this source does contribute some seed, it does not explain the great mass of reproduction, which, by its mosaic occurrence, demonstrates conclusively the impossibility of its having come from overhead seed distribution subsequent to the fire. The principal factor in reproduction after fire must be the seed stored in the duff.

UPPER CISPUS BURN, A SINGLE BURN ON WHICH THE DUFF WAS COMPLETELY DESTROYED BY THE FIRE

In an area on the Upper Cispus River, Rainier National Forest, burned in 1910, there was no reproduction except in the vicinity of seed trees; and the seedlings were more numerous close to the edge of blocks of seed trees than at a distance, which is invariably the condition where migration occurs from wind-blown seed. This is a typical example of an area made barren by a single fire which completely destroys the duff and thereby precludes the possibility of reproduction from seed stored in the forest floor. The complete destruction of the duff may have been due not so much to an unusually intense fire as to the extreme lightness of the dry volcanic soil of the region, which is easily "burned out" by ground fire. The conditions found on this area corrorborate the conclusions reached in the study of the Columbia burn. Where the duff is completely burned, reproduction is found only in inverse numerical proportion to the distance from seed trees.

AREAS, PART OF WHICH ARE SINGLE BURNS AND PART REPEATED BURNS

The studies of the Columbia burn in 1913 established the fact that most of the reproduction which follows a single burn is due to seed which was stored in the forest floor before the fire and which retained its viability through the fire. Very often, however, burned areas are again burned, and the second fire creates many complications of the factors which influence reproduction subsequent to a single burn. In order to find out the reason for the presence or absence of reproduction following repeated burns, areas on the Rainer National Forest burned over in 1864, 1874, 1892, 1902, and 1910 were studied.

COWLITZ BURN.—The Cowlitz area was burned in 1902, and the northeastern part was reburned in 1910. The original forest consisted of Douglas fir, noble fir, western red cedar, western hemlock, and western white pine.

The most striking feature of this burn is the fairly uniform distribution of reproduction of all age classes and species on the portion of the area burned only once, as shown by Table IV.

TABLE IV.—*Classification of young growth on Cowlitz area after the burn of 1902*[a]

Species.	Distance from seed trees.	Percentage of total area examined included in each distance.	Percentage of total number of seedlings found within each distance.			Grand total percentage of all seedlings found.		
			Over 10 years.	6–10 years.	0–5 years.	Over 10 years.	6–10 years.	0–5 years.
	Chains.							
Douglas fir	Over 10	37.5	16.5	45.5	38.0	35.1	56.8	8.1
	6–10	52.9	19.6	45.3	35.1			
	0–5	9.6	24.2	36.3	39.5			
Western white pine	Over 10	100	4.8	67.0	28.2	4.8	67.0	28.2
	6–10							
	0–5							
Noble fir	Over 10	36.2	33.3	40.9	25.8	37.7	37.4	24.9
	6–10	57.2	40.0	36.1	23.9			
	0–5	6.6	20.0	40.0	40.0			
Western hemlock	Over 10	36.2	18.7	34.7	46.6	17.6	26.3	56.1
	6–10	58.1	19.2	20.0	60.8			
	0–5	5.7	10.5	30.7	58.8			
Western red cedar	Over 10	50.5	23.4	53.2	23.4	20.8	47.4	31.8
	6–10	42.9	22.2	49.1	28.7			
	0–5	6.6	7.4	27.8	64.8			

[a] Total area examined = 5.15 acres.

The uniformity of distribution of each age class and the large percentages of the 0-to-5 and 6-to-10-year-age classes seemed at first to indicate restocking by the remaining seed trees after the fire. White pine snags were found on the burned area, and green white-pine trees were found in canyons and at elevations varying from 300 to 400 feet

below the area studied and well inside the mature stand of timber; yet the white-pine reproduction is found up to the highest points of the burn, which are from 800 to 1,000 feet above where the green white-pine trees were found (Pl. 4, A). It is very evident, therefore, that the white-pine reproduction could not be due to seed produced by the seed trees remaining after the fire, but must have sprung up from the seed in the ground that survived the fire. Seed trees of the other species were found on the edge of the remaining green timber at higher elevations than the burn, and therefore could bring about the restocking of the ground by these species. Since, however, the influence of seed trees on the 1910 burn, which reburned a portion of this 1902 burn, was found to be very local, the part which the seed trees played after the first burn in restocking the ground becomes questionable (Pl. 4, B). The effect of the seed trees of the different species on the second burn is shown in Table V. As can be seen from this table, the influence of seed trees extended only for from 2 to 4 chains.

TABLE V.—*Distribution of seedlings on Cowlitz area after the burn of 1910*

Species.	Number of seedlings per acre.			
	Average of 1 and 2 chains from seed trees.	Average of 3 and 4 chains from seed trees.	Average of 5 and 6 chains from seed trees.	Average of 7 and 8 chains from seed trees.
Douglas fir	280	240	40	40
Noble fir	80	0	0	20
Western hemlock	1,640	120	80	0
Western red cedar	2,120	200	40	0

None of the white-pine seed trees left on the 1902 burn which might have influenced the area of the 1910 burn were killed by the 1910 fire, though it burned closer to them than the 1902 fire. Yet no white-pine seedlings followed the 1910 burn, while white pine reproduction of all age classes came in on the 1902 burn. This would indicate that the seed trees had little influence on the restocking of the ground after the 1902 fire.

MOUNT ADAMS BURN.—Northward and westward from Mount Adams there lies an extensive stretch of burned country, embracing altogether no less than the equivalent of three full townships, and probably much more. The greater part of this area was apparently only once burned and is now a standing forest of weather-bleached snags. The rest of the area represents a much older burn. It bears evidence of being irregularly reburned and includes large barren stretches of semiarid appearance with only decayed stumps and the crumbling remains of logs to suggest the existence of a former forest.

On the area burned only once in 1892 almost all of the timber was killed. Occasional patches in such places as near a marsh or spring were left unburned. The fire-killed trees still stand, most of them retaining their branches and some of them even fragments of their bark. These are indications of a killing but not a consuming fire. The area has very much the appearance of the Columbia burn, with one striking and consistent difference. Where the Columbia burn has a fairly dense and generally satisfactory cover of reproduction, the Mount Adams burn has very sparse and inadequate reproduction. The average per acre of all species, based on 80 contiguous acres, was 436 seedlings per acre on the Columbia burn and 56 seedlings per acre on the Mount Adams burn. This lack of seedlings in the Mount Adams burn is apparently due to the light volcanic soil, which causes a drier forest floor and consequently a more complete consumption of the litter and duff by an average fire.

The composition of the reproduction actually found in the Mount Adams burn is as follows:

			Per cent.
True firs	66	Noble	35
		Silver	31
Pines	23.6	Whitebark (*Pinus albicaulis* Engelm.)	9
		Western white	8
		Lodgepole (*Pinus murrayana*)	5
		Western yellow (*Pinus ponderosa* Laws)	1.6
Other species	10.4	Western hemlock	9
		Engleman spruce (*Picea engelmanni* Engelm.)	1
		Douglas fir	0.4

There is every reason to believe that the composition of the forest before the fire was closely in accord with these figures, although it was not possible to check this absolutely. The distribution of this reproduction over the burn was fairly even, with the natural exception that in the vicinity of green timber where the fire had obviously abated there was the usual fringe of dense reproduction.

That the distribution of reproduction was found to be independent of the location of possible seed trees indicates that here, as on the Columbia burn, the source of much of that reproduction must have been seed stored in the forest floor previous to the fire. This fundamental point is especially emphasized in the case of whitebark pine, which was found throughout the burn.

Whitebark pine produces a heavy winged seed, but the wing is retained on the cone scale when the seed is liberated, hence the distance of wind migration is very limited. However, seedlings were found at distances of more than a mile from the nearest seed trees.

A peculiar feature of the occurrence of these whitebark pine seedlings gave an early clue to a convincing explanation of their presence so far from seed trees. Throughout the burn they were found most often occurring in little clumps containing from 3 to 15 seedlings, and occasionally as many as 18 were found in a clump. The seedlings in such

clumps were always closely bunched, growing usually within a space of only 2 or 3 inches in diameter. They were most often found springing from between the spreading roots of snags close to the trunks. In age the seedlings varied from 1 to 16 years, but always the individuals of a clump were of the same age or within a year of the same age. From the location of many of the clumps at the bases of snags and from the fact that the seed is known to be a favorite food of rodents, it appears that the seeds were buried by rodents.[1] Since the seedlings occur often at distances of over a mile from seed trees of this species and since rodents would not be likely to carry seeds to all parts of the burn for such distances, it is believed that the seeds were buried either before or immediately after the fire.

The young seedlings from 1 to 5 years old must therefore be remarkable examples of delayed germination. Having been buried approximately in 1892 and having germinated in 1913 these seeds of whitebark pine exhibit the retention of viability through a storage period of 21 years. Several features of the cone and seed are calculated to aid in this delayed germination. The hard, thick-scaled cone is admirably adapted as a storehouse and, when sealed by the heat of a forest fire, no doubt serves effectively to preserve the seed. Before the seed can germinate, the cone must first open or disintegrate. When buried deeply (as by rodents) in a sealed cone, the seed will naturally be most favorably placed for protracted storage. Finally, the seed itself is large, and is well protected by a thick, hard seed coat. It is very well equipped both to resist the agents of disintegration from without and to retain life within. Of all the species dealt with, it should prove, and has proved, to be among those which are able to retain their germinability for the longest period.

The reburned area was strikingly different from the area burned only once. It was apparent that the fire here had been much more severe, because the area was noticeably bare of snags. Such snags, stumps, and logs as were present were also in a much more advanced state of decay. The reproduction in this region was markedly confined to the areas only once burned, or at most to those which were visited by one severe fire followed after a long interval by one or more surface fires. The reproduction on such areas was very open, but was occasionally dense enough to make a satisfactory cover. Named in the order of their numerical importance, the species represented were lodgepole pine, hemlock (western and mountain), western white pine, whitebark pine, noble fir, and others. These covered a range of ages from 1 to 38 years, with possibly some older trees which were seeding vigorously (Pl. 5, B, C). It was impossible to fix the age of the original fire closer than between 39 and 40 years, which would place it approximately in the year 1875.

[1] Caching of whitebark-pine seeds by blue jays has been noted by C. G. Bates at the Fremont Experiment Station in Colorado.

The reason for such sparse reproduction and for its location in patchy areas must be sought in the fact that in 1892 a second severe fire swept through the burn of 1875 in an irregular width, as most fires do.

The reproduction on the area swept over by fire for the second time averages less than one seedling per square rod, and even this figure is exaggerated by the occurrence of whitebark pine seedlings in clumps of from 6 to 14 in a single spot. There are many areas several acres in extent which are absolutely bare of coniferous growth.

Although these areas are now dry and inhospitable to tree growth, the occasional tall, standing snags which have escaped destruction attest by their size that a forest of real value once occupied the ground.

Similar conditions were found on the East Canyon Creek area where a 1910 burn followed a 1902 fire. On this area the source of scattered seedlings 1 to 3 years old was demonstrated to be seed produced by a few young trees which had escaped the previous fire and had now just reached seeding age. One such tree is shown in Plate 5, A.

The reproduction found on scattered areas which have escaped the second fire suggest that after the first fire the entire burned-over area, wherever the duff was not completely burned out, must have had a similar reproduction. Since the second fire occurred 17 years later or before the young stand could produce a large amount of seed and before the ground provided favorable conditions for seed storage, there was no stored seed from which a new stand could come up, and therefore the area covered by the second fire resulted in a barren. This point is more clearly brought out in the Tower Rock burn.

Tower Rock burn.—The Cispus fire of 1902 burned in two distinct age classes of forest, one a mature Douglas-fir forest previously untouched by fire and the other a second-growth stand of pole size of almost pure Douglas fir about 40 years old. The results which followed in the two cases were strikingly different.

In the mature Douglas-fir forest the conditions after the burn repeated practically the conditions found on the Columbia burn. There was here the same occurrence and distribution of dense and sparse reproduction independent of the position of seed trees; there was the same proportion of age classes in the reproduction, evidencing the greatest germination during one or two years after the fire; there was the same alternation of patches of the original brush cover and reproduction, outlining the limits of irregular ground fire. There was, moreover, abundant proof of the inadequacy of survived seed trees to restock a burned forest area of large extent. There were left on this burn numerous groups of living seed trees of Douglas fir and minor species ideally placed for a study of their seeding influence. In spite of the most favorable conditions of site for the germination and establishment of seedlings, it was invariably found that 1-, 2-, and 3-year-old seedlings were limited to a radius of 3 and

4 chains from such seed trees. On the other hand, seedlings 10 and 11 years old were found everywhere, even at the maximum distance from seed trees attainable in the area, 12 chains (Pl. 6, A).

The destruction of a portion of the pole-sized stand of Douglas fir (Pl. 6, B) by the fire of 1902 produced peculiar conditions. When examined in September, 1914, the ground was occupied by a dense cover of deciduous shrubs and fern which grew up through a network of dead-down logs of small diameter. Reproduction occurred on this area in spite of the heavy brush cover, but it was comparatively scarce. The reproduction, in its struggle against the surrounding brush, developed the tall, lank "shade form" common to any thicket or forest-grown plant (Pl. 7, A). The older seedlings occurred independently of the position of seed trees, but showed a tendency to be limited to moist sites, such as draws and hollows, where the germination and establishment conditions were most favorable immediately after the fire. The younger seedlings (2 to 5 years old), however, showed an increase in density in the neighborhood of seed trees. Several seedlings of this class were found dead as a result of excessive drouth and heat in open spots, but they were rarely found either living or dead at distances over 6 chains from seed trees.

The occurrence of two distinct age classes of seedlings and their position in the burn with reference to seed trees indicate here again the action of two sources of seed—namely, survived seed trees and the unburned duff of the forest floor. The reasons for the failure of seed trees to restock the burn have been discussed before. The scarcity of seedlings from duff-stored seed, however, presented a problem peculiar to this burn. The dense cover of shrubby and herbaceous growth on the area might serve to account for a scarcity or absence of seedlings from "wind-blown" seed, but it will not account for the scarcity of stored-seed seedlings. Reproduction from stored seed as a rule starts at the same time as the brush on the burn and does not come in after the brush has taken possession of the ground. Hence, it has merely to hold its own in height growth with the brush; and this it has frequently proved itself able to do.

The reason for the scarcity of reproduction from duff-stored seed must be sought in the condition of the stand. The fire burned, not in an old virgin forest, but in a very young forest, which was itself successor to a burned mature forest. The earlier fire (1860) killed most of the veteran trees which were the chief source of seed stored in the forest floor. From the stored seed of the old forest there resulted a thrifty second growth of almost pure Douglas fir. How complete this stand was could not be determined; it is likely that there were openings resulting from ground fire in parts of the original burn. In 1902, at an age when this young forest was seeding but long before it had been able to reestablish most favorable conditions of the forest floor for the duff storage of its seed, this forest, too, was destroyed by fire. In the hot fire of 1902

some of the duff was undoubtedly burned, and consequently some of the stored seed. The result of this combination of circumstances was the occurrence, as was found, of scattered, inadequate reproduction amid a rank growth of deciduous brush and weeds. The reproduction was more plentiful in moist or depressed spots. These had an accumulation of duff which in a large measure escaped the ground fire and provided most favorable conditions for the germination and establishment of seedlings after the fire.

The findings on the burns studied on the Rainier National Forest corroborated those established on the Columbia burn. They brought out also additional facts regarding the effect of the conditions of the original stand upon the reproduction that follows after the fire.

When reproduction which follows a burn is destroyed by fire before it reaches seeding age, a denuded area results if the area lies outside the influence of seed trees.

Where a stand of young growth is destroyed by fire shortly after it has reached seeding age, the result is, as a rule, a thin stand of reproduction. If the fire is severe enough to destroy all seed stored in the forest floor or in cones, then it results also in a barren. The reason for the light reproduction is found in the small accumulation of duff since the previous fire and the greater liability to drouth and consumption by fire, and in the small accumulation of seed in the duff owing to the limited seed production by the young trees.

The sparseness or entire lack of reproduction after a second fire in a young stand of timber leads to the conclusion that the source of seed from which the reproduction originated after the first fire was already on the area and did not come from outside; it points also to the great danger of fires in young stands of timber before they have begun to bear plentifully and before normal leaf litter has accumulated on the ground as a storage reservoir for the seed.

GERMINATION OF SEED STORED IN DUFF

The accumulation of seed in the forest floor is no longer a theory, but has been found to be an actual condition by an analysis of the duff, which revealed from ½ to 2 full seeds of Douglas fir, western white pine, and associated species per square foot. Of course, the age of these seeds could not be determined, and the depth to which they were buried can not be taken as an index as to how long they had been there. Very probably the greatest factor in storing seed is rodent activity, by which seeds are buried at various depths and forgotten.

The accumulation of seed over a period of years can prove advantageous only if the stored seed retains its viability. With regard to this, each species possesses a dormancy habit of its own, and these habits have been growing more familiar to the forester through nursery observation and experiment. Douglas fir sown in seed spots has been found

to yield higher germination during the third season than during the first and second seasons combined. In the Wind River Nursery seed bed, germination of Douglas fir has continued through three seasons. Western white pine has often produced better germination during the second season after sowing, even under the best germinating conditions.[1] Juniper is difficult to germinate without special treatment. To some extent the rate of germination in nursery seed beds is controlled by the depth of soil cover.

With conditions such as these obtaining in regular nursery practice, it is not at all surprising that germination should be delayed under the forest cover. The cool shaded layers of leaf mold and general duff of the forest floor, which in the virgin Cascade forests seldom feel the warmth of the sun, constitute an ideal natural storage medium. Under conditions so unfavorable to germination and so favorable to its retardation, it can easily be imagined that the germination of forest tree seeds can be delayed to the limits of their various powers of dormancy.

On the Columbia burn, owing to the probability of seed accumulation for several years and to the possibility of there having been a general seed year just previous to the fire, it was not possible to determine absolutely how long the seed lay dormant. However, from the year of the fire until the date of germination (deduced from the age of seedlings found) the various species showed unquestionably the following periods of delayed germination :[2]

	Years.		Years.
Douglas fir	6	Western white pine	6
Noble fir	3	Pacific yew	10
Silver fir	5	Dwarf juniper	10
Western hemlock	6		

Delayed germination is believed to explain the proportions of age classes of the reproduction found in the open burns. Occasionally, however, single seedlings from 1 to 4 or 5 years old were found growing at great distances from seed trees in the midst of uniformly older reproduction. The presence of these "erratics" was at first a disturbing element, until it was decided that their presence could be accounted for by some one of the factors generally conceded to be responsible for the occurrence of scattered individuals of a species far beyond the normal range of that species, such as the occurrence of occasional western

[1] In this connection attention may well be called to the delayed germination experienced at the Feather River Forest Experiment Station and the Pilgrim Creek Nursery in California with the seeds of redwood (*Sequoia sempervirens* [Lamb] Emil.), white fir, incense cedar (*Libocedrus decurrens* Torr.), and sugar pine (*Pinus lambertiana* Dougl.) when sown in the nursery. Often the second season has produced more germination than the first, when the seeds were spring sown.

According to Mr. S. B. Show, seed spotting in northern California with sugar pine, Jeffrey pine (*Pinus jeffreyi*), and western yellow pine has produced very little or no germination the first season, whereas the second season a number of seedlings were found in the seed spots, and sugar pine has produced a good stand from germination the third season after sowing.

[2] The ability of seed to retain its viability is shown further by the results of Beal (1–5); Ewart (6); Harrington (7); Nobbe and Haenlein (8); Rees (9); and others, although their work was not with forest-tree seed.

Reference is made by number to "Literature cited," p. 26.

yellow pines in the true Douglas-fir type of the west slope. These agencies need only be stated to be understood.

Whirlwinds.—Sudden powerful gusts of wind with unusual lifting power carry a few seeds of almost any species to great distances.

Birds.—Birds deposit undigested seeds at long distances from the parent trees. This is especially true of migratory birds, which move when seeds are ripe and most likely to be eaten.

Animals.—Animals transport seeds in their fur or caked in the mud of their feet.

The influence of these agencies is recognized by such authorities as Strassburger, Clements, and by ecologists generally. The common occurrence of juniper (*Juniperus virginiana* L.) and black elder (*Sambricus canadensis*) along the fence rows of the Eastern States is a typical example of seeds distributed by birds. Moreover, an added possibility, in the light of the conclusions of this study, is that occasional individual seeds may possess very unusual powers of dormancy and so cause the appearance of 1- and 2-year-old seedlings as late as 10 or 15 years after their deposit in the forest floor.

A storage test in the forest floor, under the forest canopy, of seeds of Douglas fir, silver fir, noble fir, western red cedar, western white pine, and western hemlock is in progress at the Wind River Forest Experiment Station. These tests have passed through one season with no germination under the forest canopy, which indicates favorable storage conditions. At the beginning of the second season germination tests showed that the seeds of all the species used were still viable. This is conclusive evidence that reproduction, which follows a burn of all these species, is not dependent on the seed crop which is produced during the season in which the fire occurs.

Seeds recovered from the forest floor have not been germinated by the writer. However, Mr. D. R. Brewster,[1] in charge of the Priest River Experiment Station, in northern Idaho, has recovered western-white-pine seed from the forest floor in about the same amount and has secured a germination of from 2 to 20 per cent of the total number of seeds found. The striking thing about the germination is that even with ideal greenhouse conditions the larger percentage occurred during the second year. Seeds gathered as mentioned above showed the probability of from 20,000 to 80,000 seeds per acre and a germination of from 400 to 16,000 per acre; more than this number of seedlings has been actually found on burns. These facts readily explain the occurrence of dense stands of reproduction regardless of seed trees.

With this stored seed in the forest floor, let there come a forest fire which destroys completely the forest cover over a vast area and leaves no seed trees, but in its rapid sweep fails to cover all of that area with ground fire. The main storage bulwark, the chief refrigerant, the tree canopy itself with its secondary undergrowth has been removed; and

[1] Unpublished data.

the stark, dead forest of snags offers just sufficient protection from the sun's heat and excessive evaporation to make of the forest floor an ideal germinating bed. The dormant seeds, bedded in the unburned duff, are stirred to life and respond to the stimulus. Germination proceeds for each species in a manner peculiar to itself; the true firs crowd over 90 per cent of their total germination into the first season after the removal of the forest; white pine reaches its highest figure during the third season; hemlock shows a similar tendency; and Douglas fir germinates probably less than half its seed during the first season.

A few years after the fire the greening of the hills in the Columbia burn, with a mantle of reproduction, arrested the attention and aroused the wonder of those who had taken for granted that this was to be a "denuded" burn, because of its large extent and the thoroughness of the burning. The occupation of the burn by reproduction was not a gradual creeping out from the surrounding bodies of green timber, but a sudden taking possession of the entire area. In ordinary wind migration 11 years (the age of this burn) would have sufficed for only the beginning of a process of reforestation that would take generations to complete. Yet within 5 years the duff-stored seed had clothed fully 80 per cent of the Columbia burn with a satisfactory tree cover.

CUT-OVER AREAS: THE EFFECT UPON RESTOCKING OF BURNING SLASH AND OF LEAVING SLASH UNBURNED

The conclusions reached with regard to the source of seed from which reproduction starts on burns have been corroborated by the study of cut-over lands about Puget Sound during 1915 and 1916. In the Douglas-fir region covered by this study the slash is left broadcast and almost invariably burned. Thus, a study of cut-over areas is only another step in the study of burns, and covers a fire which is more severe on the surface because of the débris left by logging operations.

On one area cut over in 1914, burned in the spring of 1915, and left covered with blackened logs and ashes, cones of cedar and hemlock were found almost everywhere buried in the unburned duff. The cones were papery and almost decayed, but they were still intact in shape and contained seeds with firm endosperm. Throughout this burn there were small islands which had escaped burning and which contained large numbers of cedar and Douglas-fir seedlings germinated in the fall of 1915. These islands of reproduction demonstrate the presence of seed over the area previous to the 1915 fire, and show that if the slash had not been burned the area would have been covered with a good stand of reproduction of the same species as the original forest and in about the same proportion.

Reproduction forming a satisfactory stand—that is, 300 or more seedlings per acre—was not found more than 4 chains from green timber, and usually only 2 chains in localities where the stand depended entirely

upon seed produced after the burn. On one area which had burned over twice no reproduction followed the second burn. The patches which escaped the second fire have good reproduction of Douglas fir, cedar, and hemlock of age classes which indicate they germinated shortly after the cutting, while the area reburned supports only occasional seedlings. These seedlings very likely are due to seeds carried in by winds or animals after the second burn.

At Esperance, Wash., south of Martha Lake, a 20-year-old stand of good reproduction was found following a single slash fire (Pl. 7, C). The débris was only partially consumed, and evidences of a rather light burn were apparent. At Bitter Lake, south of Esperance, a good stand of reproduction 9 years old occurred in a slash area covered by a single fire. The remaining stumps and logs are only fire scarred and burned lightly—evidences of a light slash fire. This stand of reproduction occurred at distances of 8 chains and more from green seed trees. Another area in this locality burned by a severe slash fire had a dense stand of reproduction at 8 or 10 chains from seed trees.

Excellent stands of reproduction 20 years old, Douglas fir principally, with scattered western red cedar and western hemlock, occurred along the Edmonds Road about ½ mile east of the Pacific Highway. These are examples of reproduction in unburned slash following cuttings. The stands are great distances from green seed trees, and the even-aged class establishes the fact that they all followed within a few seasons after cutting. The fact that no evidences of a slash fire and no seed trees were found at the time of the study indicates that no seed trees were in the area after cutting. Had there been any seed trees left after cutting, they would still be there, since only a small percentage of trees left after cutting are wind-thrown in this region.

The results secured by the study of cut-over areas were not so definite as those obtained on burns in virgin stands. The exact history of the areas could not be obtained, without which the interpretation of results was difficult and in many instances impossible. The history of burns in virgin forests can usually be definitely determined; but the complex conditions generally prevailing in cut-over areas as a result of man's operations, are as a rule difficult to analyze and often impossible of interpretation. Final results in this field can be obtained only by means of the permanent plot, the complete history of which is known.

CONCLUSIONS

The study of burns and cut-over areas in the Douglas-fir region of the Pacific Northwest has brought out the following facts:

(1) The distance to which seed trees are capable of restocking the ground is limited to from 150 to 300 feet. They can not, therefore, account for the restocking of the large burned areas.

(2) The irregular, dense stands of young growth are due to seed stored in the forest floor or in cones. This seed retains its viability through the fire and is responsible for the dense reproduction that springs up after the first fire.

(3) The even-aged stands of reproduction immediately following a fire, regardless of location of remaining seed trees, the irregular alternation of dense stands of reproduction with grass areas, and the failure of reproduction on areas burned over by a second fire before the stand reaches seeding age or by consuming all of the duff and precluding any possibility of seed remaining after the fire, all point to the seed stored in the duff as the principal source of seed responsible for the restocking.

(4) The ability of the seed to retain its viability when stored in the duff or when retained in cones during fires has been further demonstrated by recovering and germinating seed from duff under forest conditions and by recovering and germinating seed from cones which passed through a crown fire.

PRACTICAL VALUE OF THE RESULTS

The fundamental facts of seed storage and viability brought out by this study have thrown new light on the whole question of natural reproduction.

The even-aged second growth stands of Douglas fir which are the general rule throughout the Pacific Northwest are due to seed stored in the ground. It has been clearly shown that these even-aged stands could not be produced by the seed scattered by the remaining seed trees. The distance of effective migration during each generation is usually only from 150 to 300 feet, varying with the adaptation of the seed for wind distribution. Migration due to other agencies than wind is responsible for individual seedlings far from the parent tree. Such individual seedlings, however, are of no practical significance in restocking large areas.

The establishment of a forest by means of wind-disseminated seed is a slow process; and with only this means of succession practically all of the large burns would be denuded areas or would support but a few scattered trees, until several generations of these trees, grown within these areas, could again restock them. This would inevitably produce an uneven-aged and irregular forest; yet the stands which follow most of the burns are even-aged. When a forest is destroyed by fire or cutting and is replaced simultaneously over large areas, the succession depends upon the seed produced at the time of or before the destruction of the forest and the ability of the seed to retain its viability through the period of destruction, whether by fire or cutting. This form of succession is the replacement of a forest almost immediately by the same species which comprised the original stand and usually in the same proportions.

Since the seed must be produced by the stand before it is destroyed, the age at which different species begin to produce seed is of the utmost importance. It varies greatly, and this variation alone is often the controlling factor in determining the composition of the second growth. For example, when western white pine, Douglas fir, and knobcone pine (*Pinus attenuata* Lemmon.) appear in a mixed stand which is destroyed by fire, all of these species may again appear in the next stand; but if this second growth is destroyed by fire when it is from 10 to 12 years old the next stand will consist principally, if not wholly, of knobcone pine. The knobcone pine begins producing seed when it is 6 years old and is producing good crops of seed at 10 years; while the white pine and Douglas fir bear only occasional cones at ages under 12 years. Therefore the knobcone pine is the only species which has any seed present to produce a forest stand following the second fire. Instances of such types are the knobcone pine types on the Siskiyou National Forest.

For this same reason, fires which destroy young growth before it is of seeding age invariably produce a denuded area by precluding any possibility of immediate reproduction; hence, the great need for fire protection in young stands of timber. Areas of immature stands when destroyed by a second fire can be restocked only by the slow process of wind disseminated seed. Hence, the viability and delayed germination of forest seeds serves to explain many conditions in the virgin forest and its reestablishment after one or more fires. The nature and severity of the fire and the age of the forest are shown to be the principal factors in determining whether reproduction will or will not follow a burn in a virgin forest.

The practical value of stored seed in the forest floor for restocking cut-over areas depends on the condition in which the forest floor is left after cutting. As has been shown, the duff must not be burned or all of the seed is destroyed. In order to avoid the destruction of the duff, it is necessary to pile the slash and burn the piles when the fire will not spread over the entire surface of the ground. This method has proved satisfactory in the white-pine region of Idaho, where piling of slash is feasible. In the Douglas-fir region of the coast the piling of slash would not be practicable because of the large amount of débris and the consequent cost. The large percentage of the surface which would of necessity be burned over even by pile burning would reduce the value of the operation for conserving seed stored in the duff, which is usually all destroyed by broadcast burning of slash.

In regions where broadcast burning of slash is the only practical method of disposing of the débris left after logging, the seed trees after all may have to be depended upon to reseed the area, in which case it will be necessary to know just how much seeding can be expected from such seed trees.

Areas with about two seed trees left for every 3 acres have been studied, but the results are questionable because the age classes and distribution of seedlings which came in after the slash fire indicated that the seedling originated from stored seed. In order to determine the effect of seed trees, the complete history of the area will have to be obtained by the permanent-plot method.

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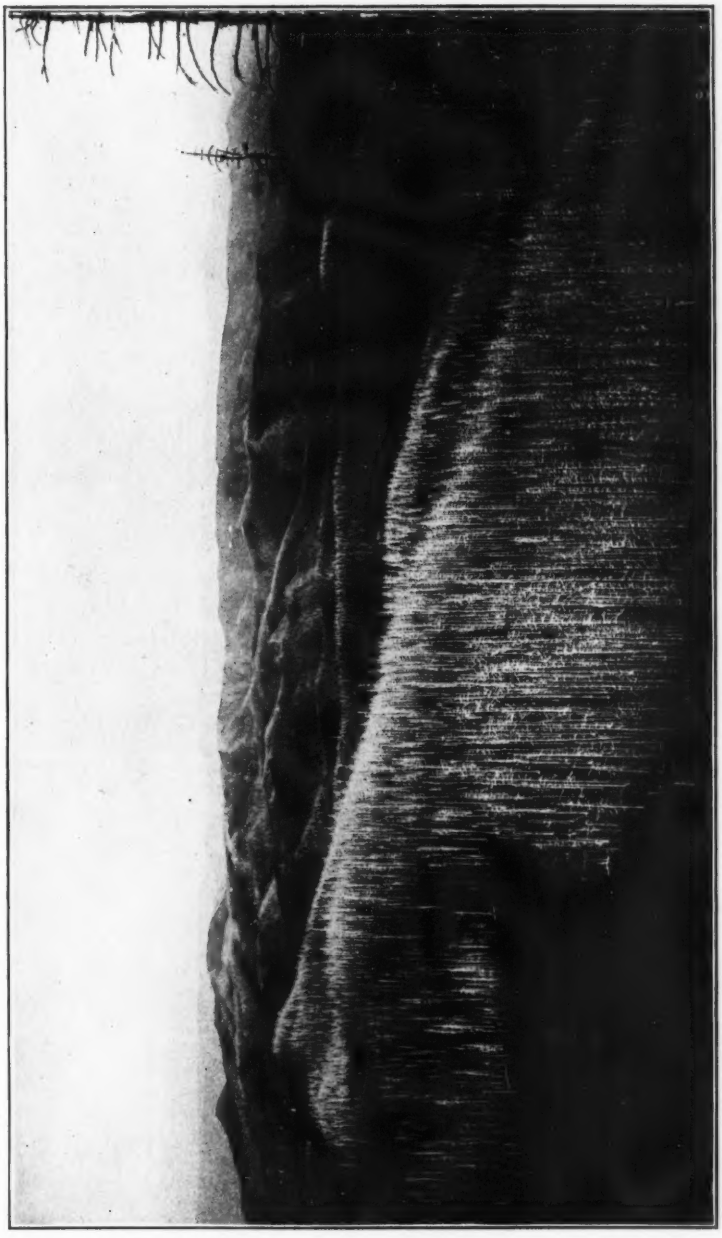
PLATE 1

A general view of a representative portion of the Yacolt Burn of 1902, Columbia National Forest, looking southward from Lookout Mountain. The entire burn covers a total of 604,000 acres. Mount Hood is shown on the horizon 30 miles distant; the gorge of the Columbia River in the upper left corner. No green timber is in sight, yet there is reproduction growing among the snags over this entire area. Photographed by Wernstedt, 1912.



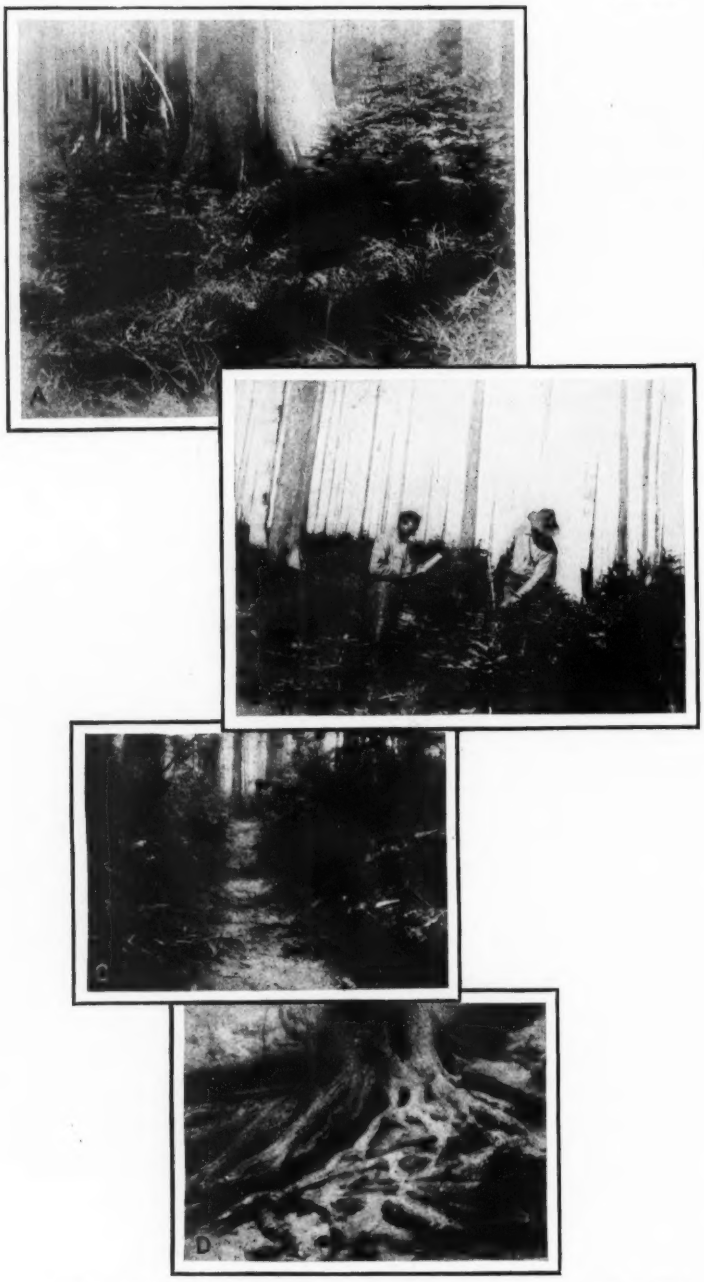

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PLATE 2

A.—"Interrupted" reproduction of noble fir on the west slope of Lookout Mountain. Note the clear-cut line between dense reproduction and grass areas. The 11-year-old seedlings here shown average about 30,000 per acre, yet these dense patches are contiguous with areas absolutely barren of seedlings. The grass areas mark the extent of ground fire; the seedlings grow where ground fire did not work. Photographed in Columbia National Forest, 1913.

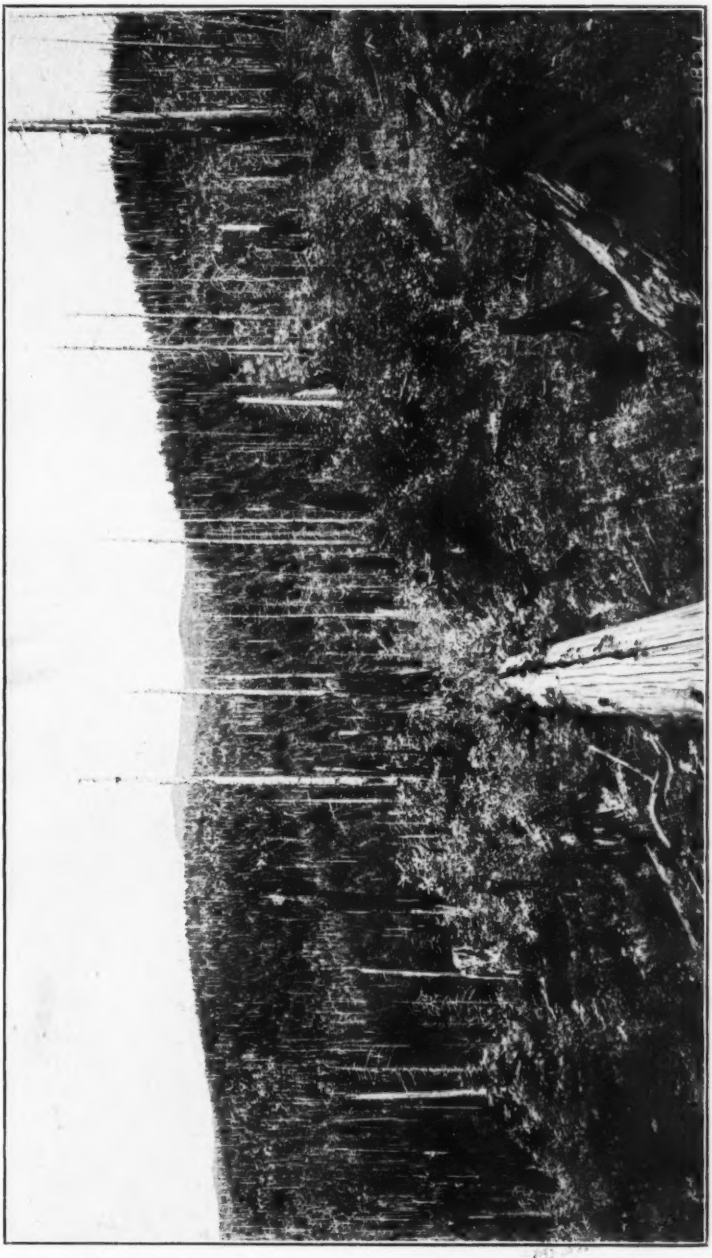
B.—The picture shows the method of measuring the height of the seedlings by means of a graduated stick which was used also in determining the width of the transect, 8¼ feet. A representative stand of noble- and silver-fir reproduction on the northeast slope of Lookout Mountain. Photographed in Columbia National Forest, 1913.

C.—A fire line cut through 18 inches of litter and duff, Foss River fire, September, 1914, Snoqualmie National Forest.

D.—This picture was taken just inside the fire line, about 15 feet from the upper picture. At the time of the fire, September 2, the forest floor was very dry and the duff was completely consumed in many places. Many trees fell after the fire because of the exposure and burning of the roots. Reproduction does not occur on such areas except near seed trees.

PLATE 3

A 20-year-old stand of Douglas fir (with white pine and others) which succeeded a single fire. No seed trees are in sight and none were left after the fire. Note the varying density of the reproduction traceable to several causes, but chiefly to the action of ground fire. Photographed near Paradise Ridge, Columbia National Forest, by Wernstedt, 1912.



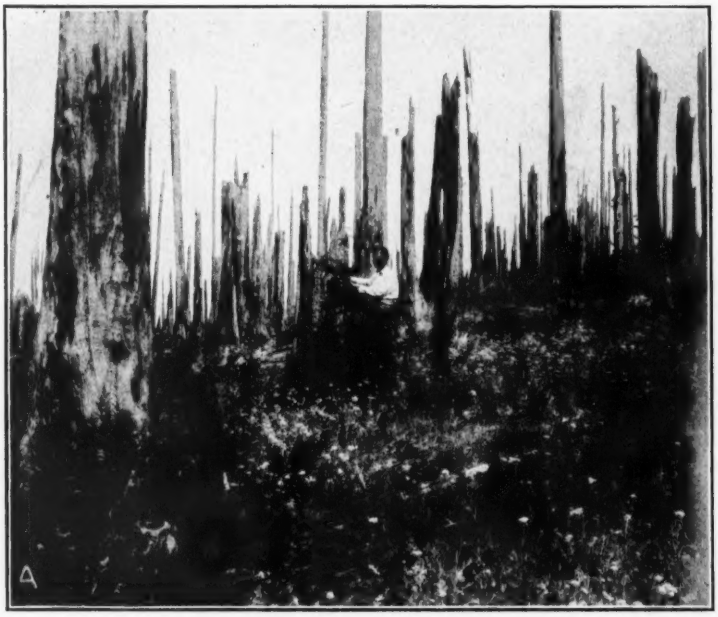

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PLATE 4

A.—Reproduction in a 1902 burn of the Cowlitz area, about 10 chains from the nearest seed trees. White-pine seed trees are nearly ¼ mile distant and are 800 feet below this area. Species shown are white pine (left), Douglas fir (center), noble fir (right). The stand on this slope is uniformly open, but will be sufficient ultimately to develop a satisfactory forest.

B.—Results of a 1910 fire following a 1902 burn. A practically denuded area. The reproduction which followed the fire had not reached seeding age when it was destroyed by the second fire. Note the dead young stand killed in 1910. Photographed in Rainier National Forest, July, 1914, on Cowlitz area.

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PLATE 5

A.—Douglas fir, 16 years old, which has been producing seed since its fourteenth year. Photographed on Rainier National Forest on East Canyon Creek, 1914.

B.—A clump of reproduction which escaped a 1910 fire (Upper Cispus, Rainier National Forest). The white pine, bearing seven cones, was 15 years old. Photographed in 1914.

C.—A clump of true firs which escaped all fires, surrounded by a small area of reproduction which resulted from 1875 fire, but was injured, and some of it destroyed by subsequent fires, notably that of 1892. Photographed in Rainier National Forest, 1914.

D.—A barren waste left where the fire of 1892 followed the fire of 1875. A striking illustration of the limit of seeding distance of green timber into an open burn. The camera station is well beyond the farthest wind-cast seed. Seedlings from such seed were not encountered until within 5 chains of the timber shown. Photographed in Rainier National Forest, 1914.

A
B
C
D

A

B

PLATE 6

A.—Reproduction resulting from a single fire in a typical mature Douglas fir forest. This is an example of what is usually found on good sites where ground fire has not been at work during the general conflagration. A fine stand of Douglas fir and associate reproduction in the "old forest" portion of the Tower Rock burn of 1902. Photographed in Rainier National Forest, 1914.

B.—Homesteaders clearing in an alder "bottom" surrounded by second growth Douglas fir. This even-aged uniform stand of Douglas fir followed a virgin forest fire of about 1860. The charred stubs in the foreground and the tall, bare snags rising above the second growth are remnants of the former forest. The burned area of this young forest in the 1902 fire at Tower Rock was not succeeded by dense reproducion as was the burned area of the virgin stand. Photographed in Rainier National Forest, 1914.

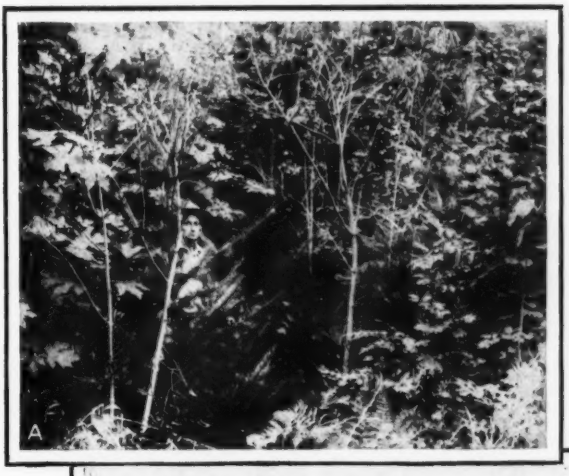
PLATE 7

A.—Douglas-fir reproduction in the brush thickets of the Cispus burn, Rainier National Forest. In their struggle to keep abreast of the surrounding brush, the coniferous seedlings make tremendous height growth and very little diameter growth. The result is the slender "shade-form" reproduction here shown. These trees are holding their own and will soon overreach the crowding brush; in the end they will dominate and completely subdue it. The deciduous growth shown includes Oregon maple, vine maple, dogwood, alder, brake fern, and fireweed. Photographed in 1914.

B.—A 1902 fire followed by a 1910 fire, photographed in 1915, Oregon National Forest, near Summit R. S. Note the sharp boundary line of the second fire. The dense reproduction succeeded the fire of 1902 and proved an effective barrier to the fire of 1910. This stoppage of fire by dense reproduction is a matter of frequent occurrence.

The picture shows also a striking comparison of duff-stored versus wind-blown seed as a source of reproduction. The dense, even-aged reproduction at the left resulted from duff-stored seed following a first burn in virgin forest. The scattered few, uneven-aged, young seedlings to the right resulted from seed blown out since 1910 from a group of seed trees from beneath which this picture was taken. The scrubby reproduction to the left was seeded from the same source, since 1902, in an opening left barren of "stored-seed reproduction" on account of ground fire. It can be readily appreciated how slow will be the reforestation of the reburned area, which is now altogether dependent upon the few seed trees which have survived both fires. When the 13-year-old stand reaches seeding age it will, of course, contribute its seed to the same purpose, within the limited range of its influence. Such a process could not conceivably have produced the beautiful uniformity in density and age which is exhibited by the 13-year-old stand here pictured.

C.—Reproduction 20 years old, at Esperance, Wash. The stand shown followed a light slash fire. In the immediate foreground a second fire occurred. The area covered by the second fire has no reproduction. Puget Sound cut-over studies. Photographed in 1915.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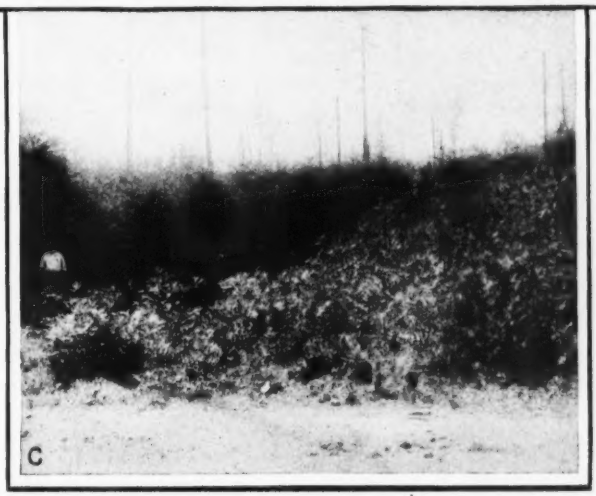
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A NEW PARASITIC NEMA FOUND INFESTING COTTON AND POTATOES

By N. A. Cobb,

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INTRODUCTION

The new species of Tylenchus described below first came to the attention of the writer in 1911, when it was found infesting rootstocks of violets (*Viola* spp.) in New York. Practically all the morphological data given herein were obtained at that time; later examinations have, for the most part, been merely confirmatory. Since its discovery this nema has again and again come to notice, first on one plant, then on another, until it is now known to infest violets, cotton roots (*Gossypium* spp.), potatoes (*Solanum tuberosum*), and the roots of camphor (*Cinnamomum camphora*) over an area in the United States extending from Florida to New York and as far west as Michigan.

It injures all the plants upon which it has been found, and, though the extent of the possible damage is not yet fully ascertained, it has been sufficient to cause growers to make inquiry concerning the origin of the injuries they were suffering. The occurrence of this parasite on potatoes is of unusual interest, for the reason that any pest found upon potatoes—at any rate one whose lesions are similar to those of *Tylenchus penetrans*—is likely to become widely disseminated unless special preventive measures are adopted. Experience emphasizes the very grave danger of spreading serious pests in seed potatoes. If noninfested land be seeded with infested potatoes, the result is, in effect, the planting out of the pest under conditions very favorable to its increase.

Unfortunately our knowledge of nemas, especially those attacking the roots of plants, is relatively very meager, and in the possession of but few. First or last, the existence of root diseases caused by these organisms comes to the attention of numerous observers, who, not having the necessary literature at their command and not knowing to whom to send specimens, often let the matter drop without adequate investigation. As it is very desirable to know more about the frequency of this pest, its host plants, the extent of the damage done by it, on what plants and at what seasons the damage is greatest, and in what kind of soil it is most active, this preliminary note aims to enlist the services of such observers.

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The illustrations have been very carefully prepared, and with their aid almost any careful microscopist should be able to identify the species. For this purpose it is advisable to use living specimens under sufficient pressure to prevent active motion. This method will give somewhat exaggerated width measurements, for which due allowance should be made. To see all the features shown, requires the use of an immersion lens under favorable conditions.

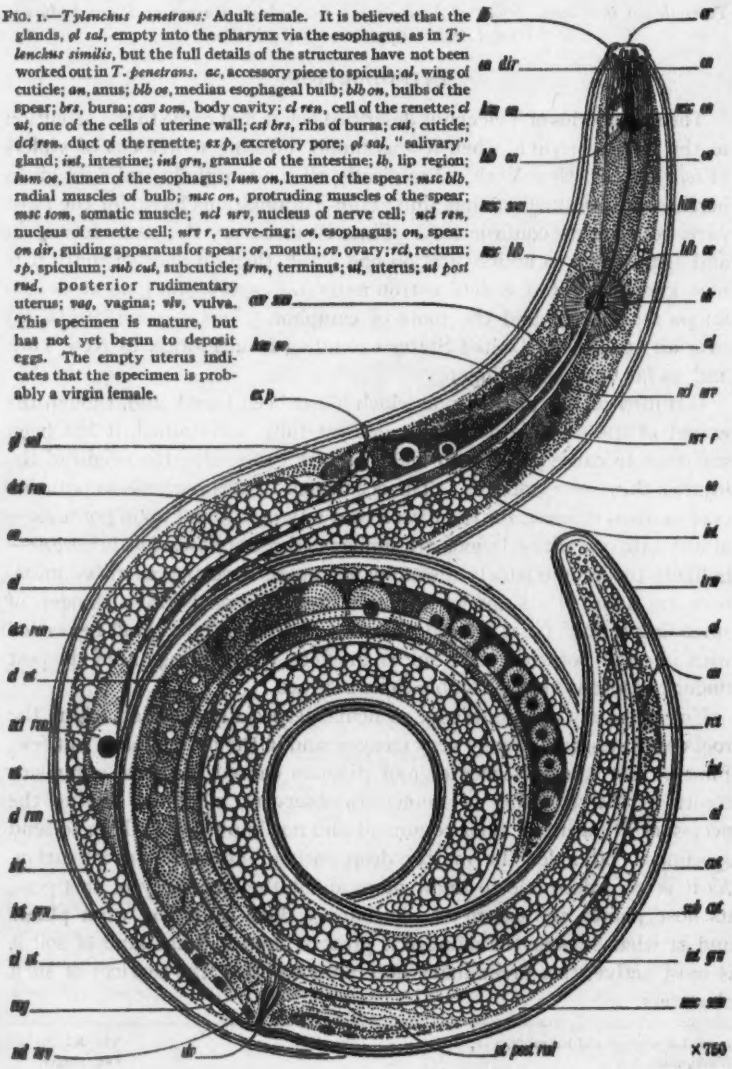

FIG. 1.—*Tylenchus penetrans:* Adult female. It is believed that the glands, *gl sal*, empty into the pharynx via the esophagus, as in *Tylenchus similis*, but the full details of the structures have not been worked out in *T. penetrans*. *ac*, accessory piece to spicula; *al*, wing of cuticle; *an*, anus; *blb oe*, median esophageal bulb; *blb on*, bulbs of the spear; *brs*, bursa; *cav som*, body cavity; *cl ren*, cell of the renette; *cl ut*, one of the cells of uterine wall; *cst brs*, ribs of bursa; *cut*, cuticle; *dct ren*, duct of the renette; *ex p*, excretory pore; *gl sal*, "salivary" gland; *int*, intestine; *int grn*, granule of the intestine; *lb*, lip region; *lum oe*, lumen of the esophagus; *lum on*, lumen of the spear; *msc blb*, radial muscles of bulb; *msc on*, protruding muscles of the spear; *msc som*, somatic muscle; *ncl nrv*, nucleus of nerve cell; *ncl ren*, nucleus of renette cell; *nrv r*, nerve-ring; *oe*, esophagus; *on*, spear; *on dir*, guiding apparatus for spear; *or*, mouth; *ov*, ovary; *rct*, rectum; *sp*, spiculum; *sub cut*, subcuticle; *trm*, terminus; *ut*, uterus; *ut post rud*, posterior rudimentary uterus; *vag*, vagina; *vlv*, vulva. This specimen is mature, but has not yet begun to deposit eggs. The empty uterus indicates that the specimen is probably a virgin female.

APPEARANCES CAUSED BY THE INFESTATION

1. ON POTATOES

On potatoes the lesions are as follows: The tuber is spotted here and there, or over its whole surface, by pimples—slightly elevated, somewhat conical areas, 2 to 5 mm. across, having a roundish, broadly elliptical or quadrangular contour. Where one or more pimples run together, the contour may be considerably elongated. Near the center of each diseased area there arises a minute opening through which the young nemas escape to found new colonies. After the potatoes have been dug and have shrunken somewhat, the diseased areas may become surrounded by shallow channels, owing to the collapse of the immediately adjacent tissues, and this shrinkage may be sufficient to cause the whole of a diseased area to present somewhat the appearance of a depression (fig. 2).

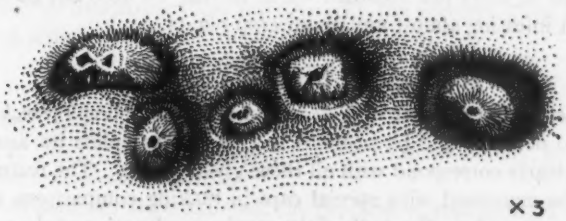

FIG. 2.—Potato pustules caused by the nema *Tylenchus penetrans*. At the left a double-headed pustule. These are from a potato that had been stored, and show the peripheral channel mentioned in the text.

2. ON VIOLETS

The rootstocks of violets infested with *Tylenchus penetrans* display brownish, somewhat collapsed areas. As in the potato, the tissues of these collapsed areas are inhabited by both sexes of the nema, and the infestation may be so intense that areas only a few millimeters in length harbor scores of specimens. The violets are very seriously injured, and as a result of careful examination, it has become quite evident that the nemas are the main cause, and in all probability the sole cause, of the injury.

3. ON COTTON ROOTS

Cotton plants infested by *Tylenchus penetrans* have been found in Georgia and North Carolina, the nemas being discovered in considerable numbers in small, diseased, colored areas on the roots. At the time the discoveries were made, the plants were not suspected of being infested; they were being examined in a general way in an effort to find out something about the nemas associated with the roots of cotton plants. No definite evidence exists that *T. penetrans* is a serious pest of the cotton plant.

4. ON THE ROOTS OF CAMPHOR TREES

Thus far no definite evidence exists that *Tylenchus penetrans* seriously injures the camphor tree. It was found in small diseased areas on the feeding roots, but not in such numbers as to seem to be the cause of trouble.

NUMBER OF HOST PLANTS

As a rule a given parasite infests but few hosts. In the genus Tylenchus and a few related genera, there are some marked exceptions to this rule, one of the most astounding of which, *Heterodera radicicola*, infests nearly 500 different species of plants. Not long ago in this Journal [1] attention was called to another species, *Tylenchus similis*, which infests such widely different plants as the banana and sugar cane. *Tylenchus penetrans* is another addition to the already rather formidable list of Tylenchi that infest a number of widely different plants; and a glance at the list of hosts just recorded warns us that we need not be surprised to find it infesting almost any of our crop plants.

IDENTIFICATION

As there are a number of Tylenchi closely resembling *Tylenchus penetrans*, no nema should be assigned to this species unless its anatomical details clearly correspond with all those given herein. The features that should be examined with special care in making comparisons are: Lip region; spear and median bulb of the esophagus; location of the excretory pore; the almost complete absence of wings;[2] the form of the tail, especially that of the male; and the size and general proportions of the body. These latter, however, may vary to some extent in accordance with the age of the specimen, and in the case of the females, according as they are or are not in a gravid condition. Some nemas, while keeping the relative proportions of many of the different parts, vary considerably in size, so that some specimens may be twice as long as others.

LOSSES

No definite information exists as to the full extent of the injury caused by this parasite upon cotton and camphor. In the case of violets the losses consist of failures, and poor growth resulting in inferior bloom. Such losses may reach an amount that constitutes a very serious handicap.

Present information indicates that the losses in the case of potatoes may sometimes be serious. The potatoes that reach a salable size often have an inferior appearance that detracts roughly 10 to 20 per cent from their market value, or even more. The infested tubers are inferior in size

[1] COBB, N. A. TYLENCHUS SIMILIS, THE CAUSE OF A ROOT DISEASE OF SUGAR CANE AND BANANA. *In* Jour. Agr. Research, v. 4, no. 6, p. 561–568, 2 fig. 1915.

[2] These are too strongly emphasized in figure 1.

as well as in quality, so that the yield is materially lessened. When the parasite infests the roots, as well as the tubers, it may cause an actual falling off in the number of tubers that are formed.

MUSCULAR POWERS: PENETRATION

When removed under the surface of water from potato pustules, the nemas sometimes lie so loosely in the tissues that they fall out three or four at a time with every movement of the dissecting needle. The structure and general appearance of this parasite discountenance the idea that its body movements are very active, at any rate after entering the host tissues. Specimens removed from potatoes exhibit only slight and weak movements.

The oral spear and the median bulb of *Tylenchus penetrans* are so well developed as to indicate clearly that the parasite is one readily capable of forcing its way into the tissues of the host plant. This fact will be appreciated by comparing these features with the corresponding features of other destructive species.

CONTROL

One important preventive measure is at once suggested by the presence of this parasite in the tubers of the potato—namely, great care in the selection of seed potatoes.

So far as potatoes are concerned, the problem of combating *Tylenchus penetrans* is very similar to that of combating the ravages due to *Heterodera radicicola;* the essence of it may be summed up in the old saying that "an ounce of prevention is better than a pound of cure." In this particular case it might almost be said that "an ounce of prevention is better than any amount of cure;" or rather, attempt at cure, for there is no assurance that land once infested with these nemas can ever be cleared of them. In the case of the average parasite, infesting but a single host, rotation of crops offers a solution in many cases at once effective and comparatively inexpensive. When, however, the parasite is capable of sustaining itself on a variety of hosts, especially if common weeds are among these hosts, the rotation of crops may not prove a thoroughly efficient remedy. It may be that no paying crop that is immune can be found. Even if such a crop exists there is the ever present menace that the parasite may maintain itself in the roots of weeds, difficult and expensive to exterminate. These facts strongly emphasize to potato growers the advisability of being very careful to plant nothing but perfectly healthy tubers.

An examination of potatoes treated with mercuric chlorid for scab showed that this treatment has a certain value in killing *Tylenchus penetrans* in the tubers. The scabby potatoes were also infested with *T. penetrans*. The vitality of the nema was much reduced and many of them appeared to have been killed by the mercuric chlorid.

SPECIFIC CHARACTERS OF THE PARASITE

Tylenchus penetrans, n. sp.—* The thin, colorless, transparent, naked cuticle is traversed by about 400 plain transverse striæ, resolvable with moderate powers. There are six amalgamated lips on which the cuticle is thickened in such a way as to have the appearance of a frontal cap. This cap is apparently built from about three ordinary striations. There are no labial papillæ. The spear is about twice as long as the lip region is wide, and is composed of two distinct regions. The posterior half is a cylindrical shaft about 1½ μ in diameter. At the very base this portion expands into a 3-lobed bulb having a diameter twice as great as that of the shaft itself. The anterior half of the spear tapers. Nothing is known concerning the lateral organs. There are no eye spots. The esophagus may be traced backward from the median bulb a distance approximately equal to the corresponding body diameter, and ends more or less indefinitely. The anterior ovary is elongated and outstretched and ends at a point as far behind the median bulb as the latter is behind the anterior extremity. The eggs occur one at a time in the uterus, and segmentation begins before they are deposited. The eggs are thin shelled, elongated, fully twice as long as the body is wide, and about one-third as wide as long. Eggs found deposited by the nemas in the tissues of the host-plant measured 78 by 25 μ, and contained fully formed embryos with well-developed spears three-fourths as long as those of the adults (fig. 1).

FIG. 3.—*Tylenchus penetrans:* Profile of the tail end and bursa of the male. The two posterior pairs of bursal ribs are very faint and easily escape observation. Compare with figure 4.

* The bursa surrounds the tail completely, springing from near the lateral lines at a point opposite the proximal ends of the two equal arcuate spicula. The general contour of the tail end of the male when viewed dorsoventrally shows no enlargement, the distance across the bursa being nowhere greater than the diameter of the body immediately in front of the anus (fig. 3 and 4).

Habitat.—Parasitic in the roots of violets, Rhinebeck, New York; roots of camphor trees, Orlando, Florida; roots of Upland cotton, Millington, North Carolina, and Statesboro, Georgia; in potatoes, vicinity of Kalamazoo, Michigan.

FIG. 4.—*Tylenchus penetrans:* Ventral view of the tail end of the male. Compare with figure 3. The two pairs of ribs near the terminus were nearly invisible in this specimen.

SUMMARY

(1) A parasitic nema, *Tylenchus penetrans*, n. sp., has been discovered infesting the tubers of the potato, the feeding roots of camphor, the rootstocks of violets, and the roots of Upland cotton.

(2) External indications of the presence of the nema are the existence on the roots or tubers of small, abnormal-looking areas, a few millimeters across, sometimes in the form of pimples, but more often in the form of slightly sunken, discolored areas. Each of these diseased areas when fully developed contains up to about 50 specimens of *T. penetrans* in various stages of growth.

* For explanation of formula, see appendix, p. 33.

(3) The geographical distribution of the pest is suggested by its presence in Florida, Georgia, North Carolina, New York, and Michigan.

(4) The occurrence of this disease under such different climatic conditions and in such a diversity of hosts makes it certain that the nema causing it is another species which, like some other destructive members of its genus, can adapt itself to widely varying conditions.

(5) As yet too little is known about this parasite to accurately estimate the damage done by it.

(6) The occurrence of the parasite in the tubers of the potato is a peculiarly significant fact and again points to the necessity of being particularly careful to plant only perfectly healthy potatoes. The mercuric-chlorid treatment of potatoes, as for scab, decreases the vitality of the nemas.

APPENDIX

Figure 5 is a diagram illustrating the decimal formula used for nematodes; 6, 7, 8, 10, 6 are the transverse measurements, while 7, 14, 28, 50, 88 are the corresponding longitudinal measurements. A formula assembling these measurements appears just below the diagram. The unit of measurement is the hundredth part of the length of the body, whatever that may be. The measurements become, therefore, percentages of the length. The absolute length of the nema is given in millimeters as a final term, in this case 1 mm.

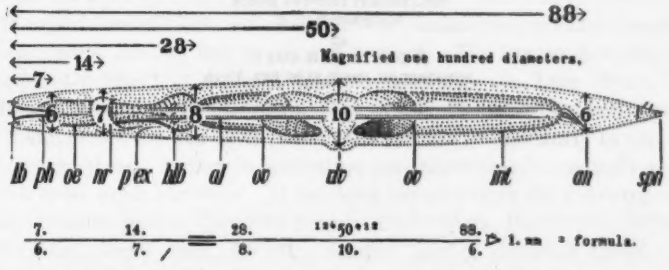

FIG. 5.—Diagram showing measurements of a nema and the corresponding formula.

The measurements are taken with the animal viewed in profile; the first are taken at the base of the pharynx, the second at the nerve ring, the third at the cardiac constriction or end of the neck, the fourth at the vulva in females and at the middle (M) in males, the fifth at the anus. The presence, situation, form, and extent of various organs is indicated in the formula by self-explanatory marks; in this case, the excretory pore, wings, spinneret, and sexual organs are so indicated. The formula thus becomes a sort of conventionalized sketch of the organism.

In this article the writer has adopted the improvement suggested by Micoletsky, and have split the measurement indicating the extent of the female sexual organs so as to show the relative proportions of the anterior and posterior branches. Thus, 50–f–5 indicates that the entire apparatus, consisting of two outstretched parts, occupies 55 per cent of the length of the nema, but that the posterior branch is a mere rudiment only five one-hundredths as long as the body.

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